TESIS DOCTORAL

Evolutionary History of Upper Jurassic Sauropods from the Lusitanian Basin (Portugal)

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ABSTRACT

ABSTRACT

Sauropod fossil record is well-represented in the Upper Jurassic of the Lusitanian Basin (Portugal). The sauropods are represented by hundreds of fossil occurrences in a sedimentary sequence ranging from the lower Kimmeridgian to the upper Tithonian. Four so far exclusive taxa were described: *Lourinhasaurus alenquerensis*, *Dinheirosaurus lourinhanensis*, *Lusotitan atalaiensis* and *Zby atlanticus*. In recent years, the interest about the Upper Jurassic sauropods of the Lusitanian Basin has risen, and several works focused on their systematic context have been published. Nevertheless, an integrative phylogenetic approach including all sauropods from the Upper Jurassic of the Lusitanian Basin was not performed yet.

The number of so far unpublished sauropod specimens is significant, with several partial skeletons collected in the Bombarral and Turcifal Sub-basins. The analysis of this material denotes for the presence of basal eusauropods (probably turiasaurs), diplodocids (closely related to Diplodocinae), basal macronarians (including camarasaurids) and titanosauriforms (including brachiosaurids). These groups are represented from the lower Kimmeridgian to the upper Tithonian. This hypothesis is corroborated by the presence of four main tooth morphotypes: heart-, spatulate-, compressed cone-chisel- and pencil-shaped.

The systematic study of the classical specimens was performed, specially focused in the type material of *Lourinhasaurus alenquerensis* and *Lusotitan atalaiensis*. The reassessment of the lectotipe of *Lourinhasaurus* has led a detailed description and a new scoring for several morphological characters. Besides the strong similarity to *Camarasaurus* species, *Lourinhasaurus alenquerensis* is here considered a valid taxon, being characterized by 13 autapomorphies. New information is provided about the *Lusotitan atalaiensis* lectotype, with the reinterpretation of the previously known elements, and the description of so far undescribed elements. The validity of this taxon is confirmed, and it is proposed a revised diagnosis. *Lusotitan* shares with the members of Brachiosauridae the presence of dorsoventrally compressed middle caudal vertebrae, pronounced deltopectoral crest, and short ischiatic contribution to acetabulum. A new sauropod specimen found in Valmitão (Lourinhã), from the Praia de Amoreira-Porto Novo Formation, is also described (SHN 181). It corresponds to a single individual composed by axial and appendicular elements. It shows an exclusive combination of characters (some of them unique for Upper Jurassic sauropods) and represents a new sauropod taxon. The Vale de Frades humerus is attributed to cf. *Duriatitan humerocristatus*.

The proposed phylogenetic analysis includes together for the first time *Lourinhasaurus*, *Dinheirosaurus*, *Lusotitan* and *Zby*, but also all the known Spanish Upper Jurassic sauropods. This phylogenetic hypothesis is based on a dataset composed by 95 taxa and 464 morphological characters. It recovers *Zby* as a turiasaur (the sister taxon of *Turiasaurus*); *Dinheirosaurus* and the so far unpublished specimen SHN (JJS) 177 as diplodocine diplodocids more derived than *Supersaurus*, *Tornieria* and *Kaatedocus* (SHN (JJS) 177 is identified as the sister taxa of *Diplodocus*); *Lourinhasaurus* as a camarasaurid (the sister taxa of *Camarasaurus*); *Lusotitan* as a brachiosaurid titanosauriform; and SHN 181 as a non-titanosauriform Macronaria.

The Portuguese Upper Jurassic fauna of sauropods shows some affinities with the synchronic North American fauna, sharing the presence of camarasaurids, diplodocines and brachiosaurids. Some of these taxa (*Dinheirosaurus*, SHN (JJS) 177 and *Lourinhasaurus*) are more closely related to North-American forms than to the Gondwanan ones. The closer relationship among Portuguese and North-American forms can be explained by and a more recent common history of these territories. On the other hand, Turiasauria is probably restricted to the European territory during the Upper Jurassic.

RESUMEN

El registro fósil de saurópodos en el Jurásico Superior de la cuenca lusitánica (Portugal) es abundante. Los saurópodos están representados por centenares de hallazgos de restos fósiles en una secuencia sedimentaria datada como del Kimmeridgiense inferior al Titoniense superior. Cuatro taxones hasta ahora exclusivos del registro portugués han sido descritos: *Lourinhasaurus alenquerensis*, *Dinheirosaurus lourinhanensis*, *Lusotitan atalaiensis* y *Zby atlanticus*. Recientemente, el interés sobre los saurópodos del Jurásico Superior de la cuenca lusitánica se ha incrementado y se han publicado varios estudios enfocados en su posición sistemática. Sin embargo, no se había realizado hasta ahora un análisis filogenético integrando todos los taxones del Jurásico Superior de la cuenca lusitánica.

Se reconoce aquí un número relevante de especímenes inéditos del Jurásico Superior de la cuenca lusitánica asignables a Sauropoda, con varios esqueletos parciales recolectados en las sub-cuencas de Bombarral y Turcifal. El estudio sistemático de este material permite identificar la presencia de eusaurópodos basales (incluyendo turiasaurios), diplodocinos, macronários basales (incluyendo camarasáuridos) y titanosauriformes (incluyendo braquiosáuridos). Estos grupos de saurópodos se encuentran homogéneamente representados desde del Kimmeridgiense inferior hasta el Titoniense superior. Esta hipótesis es corroborada por la presencia de cuatro morfotipos de dientes.

Se ha desarrollado un estudio sistemático del material clásico de saurópodos del Jurásico Superior de la cuenca lusitánica, con especial énfasis en la revisión del material tipo de *Lourinhasaurus alenquerensis* y *Lusotitan atalaiensis*. La descripción detallada de *Lourinhasaurus* ha generado nueva información que ha sido incorporada en las matrices de datos morfológicos. A pesar de su estrecha semejanza morfológica con las especies de *Camarasaurus*, *Lourinhasaurus alenquerensis* se considera un taxón válido, soportado por trece autapomorfías. Se han obtenido nuevos datos sobre el lectotipo de *Lusotitan atalaiensis*, con la reinterpretación de varios de sus elementos y la descripción de huesos hasta ahora por describir. Se confirma la validez de *Lusotitan* y se propone una nueva diagnosis. *Lusotitan* comparte con los miembros de Brachiosauridae la presencia de caudales medias dorsoventralmente comprimidas, cresta deltopectoral pronunciada y una corta contribución isquiática en el acetábulo. Se describe un nuevo espécimen (SHN 181) de Valmitão (Formación Praia de Amoreira-Porto Novo). Este individuo está compuesto por elementos axiales y apendiculares y muestra una combinación exclusiva de caracteres (incluyendo algunos caracteres no compartidos con el resto de los saurópodos conocidos en el Jurásico Superior), por lo que se considera un nuevo taxón. El húmero de Vale de Frades se atribuye a cf. *Duriatitan humerocristatus*.

Se ha realizado un análisis filogenético, basado en un matriz con 95 taxones y 464 caracteres morfológicos. Esta matriz incorpora por primera vez a *Lourinhasaurus*, *Dinheirosaurus*, *Lusotitan* and *Zby*, junto con los taxones del Jurásico Superior español. La hipótesis filogenética obtenida considera a *Zby atlanticus* como un miembro de Turiasauria (constituyendo el grupo hermano de *Turiasaurus*), *Dinheirosaurus* y el ejemplar hasta ahora inédito SHN (JJS) 177 como diplodocinos diplodócidos más derivados que *Supersaurus*, *Tornieria* y *Kaatedocus* (SHN (JJS) 177 es reconocido como el grupo hermano de *Diplodocus*), *Lourinhasaurus* como camarasáurido (siendo el taxón hermano de *Camarasaurus*), *Lusotitan* como braquiosáurido titanosauriforme y SHN 181 como macronario basal.

Las faunas de saurópodos del Jurásico Superior portugués presentan algunas afinidades con las faunas sincrónicas de América del Norte, compartiendo la presencia de camarasáuridos, diplodocinos y braquisáuridos. Algunos de estos taxones (*Dinheirosaurus*, SHN (JJS) 177 y *Lourinhasaurus*) están más estrechamente relacionados con las formas norteamericanas que con las gondwánicas. Esto puede explicarse como resultado de un contacto faunístico más reciente entre estos dos territorios. El registro de Turiasauria, por el momento, probablemente permanece restringido al territorio europeo durante el Jurásico Superior.

RESUMO

O registo fóssil de saurópodes no Jurássico Superior da Bacia Lusitânica é abundante. Os saurópodes estão representados por centenas de ocorrências ao longo de uma sequência sedimentar datada do Kimmeridgiano inferior ao Titoniano superior. Quatro táxones foram descritos a partir do registo fóssil português: *Lourinhasaurus alenquerensis*, *Dinheirosaurus lourinhanensis*, *Lusotitan atalaiensis* e *Zby atlanticus*. Nos últimos anos vários estudos foram publicados sobre os saurópodes do Jurássico Superior português, especialmente no que diz respeito à sua posição sistemática. Contudo, uma análise filogenética integrada de todos os táxones do Jurássico Superior da Bacia Lusitânica estava por realizar.

Através do presente estudo foi possível identificar um número significativo de espécimes inéditos provenientes do Jurássico Superior da Bacia Lusitânica atribuíveis a Sauropoda, com vários esqueletos parciais recolhidos nas Sub-bacias do Bombarral e Turcifal. O estudo sistemático deste material permitiu reconhecer a presença de membros basais de Eusauropoda (incluindo Turiasauria) e Macronaria (incluindo Camarasauridae), e membros de Diplodocinae e Titanosauriformes (incluindo Brachiosauridae). Estes grupos de saurópodes encontram-se distribuídos de forma homogénea desde o Kimmeridgiano inferior ao Titoniano superior. Esta composição faunística é corroborada pela pela identificação de quatro morfotipos de dentes.

O estudo sistemático do material clássico de saurópodes do Jurássico Superior da Bacia Lusitânica focalizou-se na revisão do material tipo de *Lourinhasaurus alenquerensis* e *Lusotitan atalaiensis*. A descrição detalhada de *Lourinhasaurus* deu origem a nova informação utilizada em matrizes de dados morfológicos. Apesar da forte semelhança morfológica com *Camarasaurus*, *Lourinhasaurus alenquerensis* foi considerado um táxon válido, caracterizado por treze autapomorfías. O estudo sistemático do lectótipo de *Lusotitan atalaiensis* possibilitou ainda reinterpretar e descrever vários elementos até ao momento pouco conhecidos, bem como, confirmar a validez de *Lusotitan* com a proposta de uma nova diagnose. *Lusotitan* partilha com os membros de Brachiosauridae a presença de vértebras caudais médias dorsoventralmente comprimidas, crista deltopectoral proeminente e acetábulo com contribuição isquiática curta. Um novo espécime (SHN 181) proveniente dos sedimentos da Formação Praia de Amoreira-Porto Novo, aflorantes em Valmitão (Lourinhã), é descrito pela primeira vez. Este individuo é composto por elementos do esqueleto axial e apendicular, e possui uma combinação exclusiva de caracteres (incluindo alguns caracteres ausentes no registo de saurópodes conhecido para o Jurássico Superior) que justifica a presença de um táxon novo. O úmero de Vale de Frades é atribuído a cf. *Duriatitan humerocristatus*.

A análise filogenética efectuada baseou-se numa matriz formada por 95 táxones e 464 caracteres morfológicos. Esta matriz incorpora pela primeira vez *Lourinhasaurus*, *Dinheirosaurus*, *Lusotitan* e *Zby* juntamente com os táxones do Jurássico Superior-Cretácico basal espanhol. A hipótese filogenética estabelecida considera *Zby atlanticus* como membro de Turiasauria (e grupo irmão de *Turiasaurus*); *Dinheirosaurus* e um exemplar ainda inédito (SHN (JJS) 177) como membros de Diplodocinae, e mais derivados que *Supersaurus*, *Tornieria* e *Kaatedocus* (SHN (JJS) 177 é reconhecido como o grupo irmão de *Diplodocus*); *Lourinhasaurus* como membro de Camarasauridae (e grupo irmão de *Camarasaurus*); *Lusotitan* com membro de Brachiosauridae; e SHN 181 como um macronário basal.

As faunas de saurópodes do Jurássico Superior de Portugal apresentam algumas afinidades com as faunas sincrónicas da América do Norte, partilhando a presença de membros de Camarasauridae, Diplodocinae e Brachiosauridae. Alguns destes táxones (*Dinheirosaurus*, SHN (JJS) 177 e *Lourinhasaurus*) estão mais estreitamente relacionados com as formas norte-americanas do que com as gondwânicas. Esta situação deverá resultar de um contacto faunístico mais recente entre a Península Ibérica e o território norte-americano. O registo fóssil de Turiasauria está, com base no conhecimento actual, restringido ao território europeu durante o Jurássico Superior.

CHAPTER 1

Introduction

1.1. INTRODUCTION

Sauropods are a group of saurischian dinosaurs, and one of the best-represented groups of Mesozoic vertebrates being recorded in all continents. Their stratigraphic record ranges from the Upper Triassic up to the end of the Cretaceous (e.g. McIntosh, 1990a; Buffetaut et al., 2000; Upchurch et al., 2004; Cerda et al., 2011). These herbivorous dinosaurs show a wide range of sizes and some of them became the biggest known terrestrial animals (e.g. Huene, 1932; Coria and Bonaparte, 1991; Gillette, 1991; Sanz et al., 1999; Royo-Torres et al., 2006; Sander et al., 2006; Lavocara et al., 2014).

In the Lusitanian Basin (Portugal), Sauropoda is a well-represented group recorded from the Upper Jurassic to the uppermost Cretaceous (Sauvage, 1897-98; Lapparent and Zbyszewski, 1957; Antunes and Sigogneau, 1992; Dantas, 1992; Antunes and Mateus, 2003). In particular, concerning the Upper Jurassic record, sauropods are the most abundant dinosaur group, with hundreds of fossil occurrences in a sedimentary sequence ranging from the Kimmeridgian to the upper Tithonian (Lapparent and Zbyszewski, 1957; Dantas et al., 1990; Dantas, 1990; Bonaparte and Mateus, 1999; Yagüe et al., 2006; Mateus, 2005; Mocho et al., 2011, 2012, 2013a, b, 2014a, b, in press; Mannion et al., 2012, 2013; Mateus et al., 2014).

At the end of the 19th century, Sauvage (1897-98) published the first sauropod occurrences in the Lusitanian Basin. In this study on the Portuguese Mesozoic vertebrate faunas, Sauvage (1897-98) recognized two Upper Jurassic sauropods: *Pelorosaurus humerocristatus* and a new species of *Morosaurus* (=*Camarasaurus*), *Morosaurus marchei*. Nowadays, *Morosaurus marchei* is considered as *nomina dubia* (Antunes and Mateus, 2003) and part of the referred material pertains to indeterminate theropods (Weishampel et al., 2004). The sauropod referred material to *Pelorosaurus humerocristatus* probably corresponds to indeterminate turiasaurians.

Later, Zbyszewski (1946) reported a new fossil-site in Pedras Muitas (Peniche) including remains of sauropod and thyreophoran dinosaurs. Lapparent and Zbyszewski (1957) carry on an important study about the Mesozoic dinosaurs of Portugal. Several new specimens were reported, highlighting the sauropods of Moinho do Carmo (Alenquer), Peralta (Lourinhã) and San Bernardino (Peniche). These authors established a new species of *Brachiosaurus*, *Brachiosaurus atalaiensis*, and a new species of *Apatosaurus*, *Apatosaurus alenquerensis*. Both genera are established based on North American and African material. The presence in Portugal of genera from the Morrison Formation suggested for an Upper Jurassic contact between North American and Iberian faunas. Lapparent and Zbyszewski (1957) also established a new species of *Astrodon*, *Astrodon pusillus*. Nevertheless, Galton (1991) revised this material, and related it to the European thyreophoran *Dacentrurus*. Lapparent and Zbyszewski (1957) supported the presence of *Pelorosaurus humerocristatus* in the Portuguese Upper Jurassic.

The systematic revision of the Portuguese sauropods and the study of several new specimens found late last century provide a new scenario for sauropod faunas of the Portuguese Upper Jurassic. The published information suggests that this group is mainly represented in the Lusitanian Basin by four exclusive forms: *Lourinhasaurus*, *Lusotitan*, *Dinheirosaurus* and the recently described *Zby* (Dantas et al., 1998; Bonaparte and Mateus, 1999; Antunes and Mateus, 2003; Mateus et al., 2014).

The material referred to *Apatosaurus alenquerensis*, including the partial skeleton found in Moinho do Carmo, was revised by Dantas et al. (1998). These authors established a new genus, *Lourinhasaurus*, proposing a new combination, *Lourinhasaurus alenquerensis*. This genus was established based on the Moinho do Carmo specimen (Alenquer) and a new specimen found in the Porto Dinheiro (Lourinhã) cliffs. Some authors suggested that *Lourinhasaurus alenquerensis* might represent a species within *Camarasaurus* (e.g. Wilson and Sereno, 1998). Previous phylogenetic hypotheses consider *Lourinhasaurus* as a basal eusauropod (Upchurch et al.,

2004), as a basal macronarian (Royo-Torres et al., 2006; Barco, 2010), or as a non-macronarian neosauropod (Royo-Torres and Upchurch, 2012; Royo-Torres et al., 2012).

After the publication of the Porto Dinheiro specimen as *Lourinhasaurus alenquerensis*, Bonaparte and Mateus (1999) established a new taxon, *Dinheirosaurus lourinhanensis*. This taxon was recognized as a member of Diplodocidae or a possible diplodocine (Rauhut et al., 2005; Whitlock, 2011; Mannion et al., 2012; Tschopp and Mateus, 2013; Tschopp et al., 2015). Mannion et al. (2012) recovered this taxon as a sister taxon of the Morrison Formation genus *Supersaurus*. Additionally, in a recent specimen-level phylogenetic analysis, this taxon was considered as a member of the *Supersaurus* genus, being proposed a new combination, *Supersaurus lourinhanensis* (Tschopp et al., 2015).

Antunes and Mateus (2003) considered that the supposed Portuguese species of the genus *Brachiosaurus* represent a new genus, establishing *Lusotitan atalaiensis*. In a recent redescription of the *Lusotitan* lectotype from Peralta performed by Mannion et al. (2013), *Lusotitan* was considered as basal macronarian, probably a brachiosaurid.

Zby atlanticus is the last established taxon for the Portuguese Upper Jurassic. The holotype was found in sediments of the Praia de Amoreira-Porto Novo Formation, in Vale de Pombas (Lourinhã, Mateus et al., 2014). This specimen was firstly considered as *Camarasaurus* sp. (Mateus, 2005) and later as *Turiasaurus riodevensis* (Mateus, 2009). Mateus et al. (2014) considered *Zby* as a member of Turiasauria, but no cladistic analyses were performed. The Turiasauria affinities of this specimen were previously noted by Mateus (2009), Royo-Torres and Upchurch (2012), Mocho et al. (2012) and Royo-Torres et al. (2014).

Several other specimens (some of them in preparation) have been published in the last years, providing a great improvement on the understanding of the composition of the Portuguese Upper Jurassic sauropod faunas, and consequently, about its evolutionary history (Antunes and Mateus, 2003; Yagüe et al., 2006; Malafaia et al., 2010; Ortega et al., 2010; Mocho et al., 2011, 2012, 2013b, c, 2014b, in press; Mannion et al., 2012). Nevertheless, hundreds of specimens deposited in the Museu Geológico (Lisboa, Portugal), Sociedade de História Natural (Torres Vedras, Portugal), Museu da Lourinhã (Lourinhã, Portugal), Museu Municipal Leonel Trindade (Torres Vedras, Portugal), Museu Municipal do Bombarral (Bombarral, Portugal), Museu Municipal de Porto de Mós (Porto de Mós, Portugal) and Museu Nacional de História Natural e da Ciência (Lisboa, Portugal) remain unpublished.

The sauropod faunas of the Portuguese Upper Jurassic are mainly composed by exclusive forms (e.g. Dantas et al., 1998; Bonaparte and Mateus, 1999; Antunes and Mateus, 2003; Mannion et al., 2012, 2013; Ortega et al., 2009, 2013; Mocho et al., 2014a, Mateus et al., 2014). Nevertheless, some faunistic groups present an amphi-Atlantic distribution with shared genera and even species such as ostracodes (Schudack, 2000), mammals (Martin, 2000) and other dinosaur groups (Pérez-Moreno et al., 1999; Escaso et al., 2007) suggesting the presence of an Upper Jurassic contact between North America and the Iberian Peninsula. The phylogenetic relationships of some taxa and specimens are still uncertain, being necessary an integrative study with all the Upper Jurassic Iberian forms, and the synchronic forms from the European record, the Morrison (USA) and the Tendaguru (Tanzania) Formations. This will allow obtaining a new phylogenetic hypothesis for the peri-Atlantic sauropod faunas during the Upper Jurassic.

1.2. INTRODUCCIÓN

Los saurópodos son dinosaurios saurisquios y uno de los grupos de dinosaurios mejor representado en el registro fósil del Mesozoico, presentes en todos los continentes en un rango estratigráfico que abarca desde el Triásico Superior hasta el final del Cretácico Superior (e.g. McIntosh, 1990a; Buffetaut et al., 2000; Upchurch et al., 2004; Cerda et al., 2011). Este grupo de

dinosaurios incluye formas herbívoras de pequeño, medio y gran tamaño, algunas de las cuales han alcanzado dimensiones colosales, correspondiendo a las mayores formas terrestres hasta hoy conocidas (e.g. Huene, 1932; Gillette, 1991; Bonaparte y Coria, 1993; Sanz et al., 1999; Upchurch et al., 2004; Royo-Torres et al., 2006; Sander et al., 2006; Lacovara et al., 2014).

Los saurópodos son uno de los grupos de vertebrados mesozoicos más abundantemente representado en la Cuenca Lusitánica (Sauvage, 1897-98; Lapparent y Zbyszewski, 1957; Dantas, 1990; Antunes y Mateus, 2003), en la que presentan un registro desde el Jurásico Superior hasta el Cretácico terminal (e.g. Antunes y Sigogneau, 1992; Antunes y Mateus, 2003). En particular, el registro de saurópodos del Jurásico Superior es el más abundante en relación al resto de grupos de dinosaurios representados. De hecho, se han identificado cientos de restos de saurópodos en una secuencia sedimentaria que abarca desde el Kimmeridgiense inferior hasta el Titoniense superior (Lapparent y Zbyszewski, 1957; Dantas et al., 1990; Dantas et al., 1992; Bonaparte y Mateus, 1999; Yagüe et al., 2006; Mateus, 2005; Mocho et al., 2011, 2012, 2013a, b, c, 2014a, b, en prensa; Mannion et al., 2012, 2013; Mateus et al., 2014).

Las primeras referencias a restos de saurópodos en la Cuenca Lusitánica se remontan a finales del siglo XIX (Sauvage, 1897-98). En el primer análisis del registro de saurópodos del Jurásico Superior portugués, Sauvage (1897-98) reconoció la presencia de *Pelorosaurus humerocristatus* y estableció una nueva especie de *Morosaurus* (=*Camarasaurus*), *Morosaurus marchei*. Estudios posteriores refutaron estas atribuciones (Lapparent y Zbyszewski, 1957; Antunes y Mateus, 2003; Upchurch et al., 2004).

Después del estudio de Sauvage (1897-98), los saurópodos del Jurásico portugués volvieron a ser tratados por Zbyszewski (1946), tras el descubrimiento del yacimiento de Pedras Muitas (Peniche), en el que se recolectaron diversos restos de dinosaurios saurópodos y tireóforos. A mediados del siglo XX, Lapparent y Zbyszewski (1957) presentaron un estudio detallado sobre las faunas de dinosaurios del Mesozoico portugués. En ese trabajo se describieron varios especímenes, destacando los saurópodos de Moinho do Carmo (Alenquer), Peralta (Lourinhã) y San Bernardino (Peniche). Además, estos autores definieron una nueva especie de *Brachiosaurus*, *Brachiosaurus atalaiensis*, y una nueva especie de *Apatosaurus*, *Apatosaurus alenquerensis*. Ambos géneros habían sido descritos a partir de material norteamericano, estando bien representados en los sedimentos jurásicos de la Formación Morrison en EEUU. La presencia en el Jurásico Superior portugués de géneros norteamericanos sugirió la posibilidad de dispersión entre las faunas de Norteamérica y la península ibérica, al menos en determinados momentos del Jurásico Superior, hipótesis corroborada recientemente (e.g. Pérez-Moreno et al., 1999). Lapparent y Zbyszewski (1957) también establecieron una nueva especie del taxón cretácico norteamericano *Astrodon* en el registro del Jurásico Superior portugués: *Astradon pusillus*. Sin embargo, posteriormente Galton (1991) reasignó ese material a otro grupo de dinosaurios (Thyreophora), siendo atribuido al género europeo *Dancentrurus*. Lapparent y Zbyszewski (1957) incluyeron a *Pelorosaurus humerocristatus* en su listado faunístico.

La revisión sistemática de varios taxones de saurópodos del Jurásico Superior portugués y el estudio de nuevos hallazgos, realizados a finales del siglo XX y en el presente siglo, han generado un nuevo escenario para estas faunas. Así, actualmente se considera que este registro estaría compuesto esencialmente por taxones exclusivos, correspondientes a, al menos, cuatro géneros: *Lourinhasaurus*, *Lusotitan*, *Dinheirosaurus* y el recientemente descrito *Zby* (Dantas et al., 1998; Bonaparte y Mateus, 1999; Antunes y Mateus, 2003; Mateus et al., 2014).

Dantas et al. (1998) establecieron un nuevo taxón, *Lourinhasaurus alenquerensis*, a partir del material previamente asignado a *Apatosaurus alenquerensis*. A esta especie se atribuyó tanto el ejemplar del yacimiento de Moinho do Carmo (Alenquer), como un nuevo individuo encontrado en los acantilados de Porto Dinheiro (Lourinhã). Sin embargo, algunos autores consideran que este género podría ser sinónimo del taxón norteamericano *Camarasaurus* (e.g. Wilson y Sereno,

1998). Los estudios cladísticos que han incorporado a *Lourinhasaurus* generalmente establecen una posición filogenética poco estable, dado que ha sido propuesto como un representante de varios clados: un eusaurópodo basal para Upchurch et al. (2004); un neosaurópodo basal para Royo-Torres y Upchurch (2012) y Royo-Torres et al. (2012) o un macronario basal para Royo-Torres et al. (2006) y Barco (2010).

Tras la publicación del material de Porto Dinheiro como perteneciente a *Lourinhasaurus*, Bonaparte y Mateus (1999) definieron un nuevo género y especie a los que asignaron este espécimen: *Dinheirosaurus lourinhanensis*. Este taxón se reconoce actualmente como perteneciente a Diplodocidae y, más concretamente al clado Diplodocinae (Rauhut et al., 2005; Whitlock, 2011; Mannion et al., 2012; Tschopp y Mateus, 2013; Tschopp et al., 2015). Mannion et al. (2012) propusieron que este taxón podría estar estrechamente relacionado con el diplodócido del Jurásico Superior de la Formación Morrison *Supersaurus* y, posteriormente, Tschopp et al. (2015) confirmaron su atribución a dicho género, proponiendo la nueva combinación *Supersaurus lourinhanensis*.

Antunes y Mateus (2003) consideraron que la especie portuguesa preliminarmente atribuida al género *Brachiosaurus* correspondía a un nuevo género, para el que establecieron la denominación *Lusotitan atalaiensis*. La reciente revisión sistemática de este taxón ha concluido que *Lusotitan* es un macronario basal, cercano al clado Brachiosauridae (Mannion et al., 2013).

Zby atlanticus es el último taxón definido para el Jurásico Superior portugués. Su holotipo y único espécimen conocido proviene de los sedimentos de la Formación Praia de Amoreira-Porto Novo, en la localidad de Vale de Pombas (Mateus et al., 2014). Dicho espécimen fue previamente considerado como *Camarasaurus* sp. por Mateus (2005) y como *Turiasaurus riodevensis* por Mateus (2009). Mateus et al. (2014) atribuyeron esta nueva forma al clado Turiasauria, sin contrastar esta atribución mediante un análisis cladístico. Esta identificación es acorde con la previamente sugerida por Mateus (2009), Royo-Torres and Upchurch (2012), Mocho et al., (2012) y Royo-Torres et al. (2014).

Además de los cuatro taxones referidos, varios especímenes (algunos todavía en preparación) han sido publicados en los últimos años, aportando una mejor comprensión de la composición faunística de los saurópodos portugueses, así como de su historia evolutiva (Antunes y Mateus, 2003; Yagüe et al., 2006; Malafaia et al., 2010; Ortega et al., 2010; Mocho et al., 2011, 2012, 2013b, c, 2014b, en prensa; Mannion et al., 2012). Sin embargo, cientos de ejemplares depositados en el Museu Geológico (Lisboa, Portugal), Sociedade de História Natural (Torres Vedras, Portugal), Museu da Lourinhã (Lourinhã, Portugal), Museu Municipal Leonel Trindade (Torres Vedras, Portugal), Museu Municipal do Bombarral (Bombarral, Portugal), Museu Municipal de Porto de Mós (Porto de Mós, Portugal) y Museu Nacional de História Natural e da Ciência (Lisboa, Portugal) siguen inéditos.

En consecuencia, se considera que la fauna de saurópodos del Jurásico Superior y de la transición Jurásico-Cretácico ibérico está mayoritariamente compuesta por formas exclusivas (e.g. Dantas et al., 1998; Bonaparte y Mateus, 1999; Antunes y Mateus, 2003; Mannion et al., 2012, 2013; Ortega et al., 2009, 2013; Mocho et al., 2014a, Mateus et al., 2014). Sin embargo, la presencia de taxones con distribución anfi-atlántica (a nivel genérico, e incluso a nivel especifico) como ostrácodos (Schudack, 2000), algunos mamíferos (Martin, 2000) y otros grupos de dinosaurios (Pérez-Moreno et al., 1999; Escaso et al., 2007), sugirieron la posibilidad de la existencia de dispersión de faunas entre el continente norteamericano y la península ibérica. Las relaciones filogenéticas de algunos taxones y especímenes son inciertas, siendo necesario el estudio integrado de todas las formas ibéricas junto con el de las formas sincrónicas del registro europeo, de la Formación Morrison (EEUU) y de la Formación Tendaguru (Tanzania), con el fin de proponer una nueva hipótesis sobre sus relaciones de parentesco.

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CHAPTER 2

Objectives and hypotheses

2.1. OBJECTIVES AND HYPOTHESES

The aim of this PhD Thesis is to study the evolutionary history of the sauropods from the Upper Jurassic (Kimmeridgian-Tithonian) of the Lusitanian Basin (Portugal), including the discussion of their phylogenetic, stratigraphic and paleobiogeographic implications.

General hypothesis. The Portuguese Upper Jurassic sauropod record is composed by exclusive forms: the turiasaur *Zby atlanticus*, the camarasaurid *Lourinhasaurus alenquerensis*, the diplodocid *Dinheirosaurus lourinhanensis* and the brachiosaurid *Lusotitan atalaiensis*. This record is composed by forms that are closely related to sauropods represented in the synchronous record of the Morrison Formation (USA). It is the result of a process of incipient north-Atlantic vicariance.

The main objectives of this thesis are based in the study of several specimens collected in the Upper Jurassic sediments of the Lusitanian Basin:

- Systematic revision of the classical material attributed to sauropods from the Upper Jurassic of the Lusitanian Basin and comparison with the synchronic forms represented in the fossil record of other Iberian basins.
- Systematic study of recently published and unpublished occurrences related with sauropods from the Upper Jurassic of the Lusitanian Basin and comparison with the synchronic forms represented in the fossil record of the Iberian Peninsula and the peri-North Atlantic realm.
- Phylogenetic analysis of the Portuguese Upper Jurassic sauropods considering all established taxa for the Iberian Peninsula and proposing an updated phylogenetic hypothesis integrating the sauropod fossil record of North America, Africa and Europe.

The main hypothesis and objectives of this thesis involve the development of several minor hypotheses and objectives.

Hypothesis 1.a. *Lourinhasaurus alenquerensis* is an exclusive form of the Portuguese Upper Jurassic record. Hypothesis 1.b. *Lourinhasaurus alenquerensis* is a member of Camarasauridae. Hypothesis 1.c. *Lourinhasaurus alenquerensis* is closely related to *Camarasaurus*.	Objective 1.a. Test the validity of *Lourinhasaurus alenquerensis* and proposal of a revised diagnosis for the taxon. Objective 1.b. Establish a new phylogenetic approach for the *Lourinhasaurus alenquerensis* lectotype. Objective 1.c. Systematic review of the classical material previously referred to *Lourinhasaurus alenquerensis*, coming from the localities of São Bernardino, Areia Branca, Porto das Barcas, Salir de Matos, Alcobaça, Praia de Santa Cruz, Chiqueda de Cima, Vale Frades, Foz do Arelho, São Mamede, Torres Vedras and Ourém (Upper Jurassic, Lusitanian Basin).
Hypothesis 2.a. *Lusotitan atalaiensis* is an exclusive form of the Portuguese Upper Jurassic record. Hypothesis 2.b. *Lusotitan atalaiensis* is a member of Brachiosauridae.	Objective 2.a. Test the validity of *Lusotitan atalaiensis* and propose a revised diagnosis for this taxon. Objective 2.b. Establish an updated phylogenetic approach for the *Lusotitan atalaiensis* lectotype. Objective 2.c. Systematic review of the classical material previously referred to *Lusotitan atalaiensis*, coming from the localities of Areia Branca, Porto Novo (Maceira), Alcobaça, Cambelas and Praia das Almoinhas? (Upper Jurassic, Lusitanian Basin).

Hypothesis 3.a. *Dinheirosaurus lourinhanensis* is an exclusive form of the Portuguese Upper Jurassic record. Hypothesis 3.b. *Dinheirosaurus lourinhanensis* is a member of Diplodocinae.	Objective 3.a. Test the validity of *Dinheirosaurus lourinhanensis* and propose a revised diagnosis for this taxon. Objective 3.b. Establish an updated phylogenetic approach for *Dinheirosaurus lourinhanensis*.
Hypothesis 4.a. *Zby atlanticus* is an exclusive form of the Portuguese Upper Jurassic record. Hypothesis 4.b. *Zby atlanticus* is a member of Turiasauria.	Objective 4.a. Test the validity of *Zby atlanticus* and propose a revised diagnosis for this taxon. Objective 4.b. Establish an updated phylogenetic approach for *Zby atlanticus*.
Hypothesis 5. The specimen SHN 181 from Valmitão (Lourinhã) corresponds to a new taxon.	Objective 5. Systematic study of SHN 181, a so far unpublished sauropod specimen, found in the Upper Jurassic Praia de Amoreira-Porto Novo Formation of Valmitão (Lourinhã).
Hypothesis 6.a. The recorded sauropod paleobiodiversity of the Lusitanian Basin is composed by turiasaurs, diplodocids, camarasaurids and brachiosaurids. Hypothesis 6.b. The sauropod paleobiodiversity of the Lusitanian Basin (turiasaurs, diplodocids, camarasaurids and brachiosaurids) presents a homogenous stratigraphic and geographical distribution.	Objective 6.a. Establish a new phylogenetic approach, in a global sauropod phylogeny, of all sauropod taxa described for the Portuguese Upper Jurassic record and evaluate the paleobiodiversity of the this group in the Lusitanian Basin. Objective 6.b. Systematic analysis and stratigraphic distribution of sauropod teeth found in the Upper Jurassic sediments of the Lusitanian Basin, including heart-, spatulate-, compressed cone-chisel- and pencil-shaped teeth. Objective 6.c. Systematic analysis and stratigraphic distribution of other Upper Jurassic cranial, axial and appendicular material related to Sauropoda in the distinct sub-basins that compose the Lusitanian Basin (Bombarral, Turcifal and Arruda Sub-basins).
Hypothesis 7. The sauropod faunas of the Upper Jurassic of Portugal are composed by distinct forms that those present in the Upper Jurassic-basal Cretaceous record of Spain.	Objective 7. Compare the Upper Jurassic Portuguese and Upper Jurassic-basal Cretaceous Spanish sauropods and establish the degree of affinity of these and other sauropod taxa.
Hypothesis 8. The phylogenetic relationships between the Portuguese and the North American Upper Jurassic sauropods do not support the presence of the Upper Jurassic faunistic contacts previously proposed based on other groups.	Objective 8. Compare the Portuguese Upper Jurassic record of sauropods with the North American one, and establish their degree of affinity.

2.2. OBJETIVOS E HIPÓTESIS

El objetivo general que persigue esta tesis doctoral es proponer una hipótesis de relación de parentesco entre los dinosaurios saurópodos representados en el Jurásico Superior (Kimmeridgiense-Titoniense) de la cuenca lusitánica (Portugal) y establecer las implicaciones estratigráficas y paleobiogeográficas derivadas de su distribución.

Hipótesis general. El registro de saurópodos del Jurásico Superior portugués está compuesto por formas exclusivas: el turiasaurio *Zby atlanticus*, el camarasáurido *Lourinhasaurus alenquerensis*, el diplodócido *Dinheirosaurus lourinhanensis* y el braquiosáurido *Lusotitan atalaiensis*. Las faunas de saurópodos de la cuenca lusitánica están compuestas por formas cercanamente emparentadas con los grupos presentes en el registro sincrónico de la Formación Morrison (EEUU). Este patrón se explica como consecuencia de un incipiente proceso de vicarianza en el contexto transatlántico a finales de Jurásico.

Muchos de los objetivos asociados a esta hipótesis general se relacionan con el estudio sistemático de especímenes de saurópodos recogidos en la citada cuenca que, agrupándolos de forma cronológica, resultarían en:

- Revisión sistemática del material clásico atribuido a dinosaurios saurópodos del Jurásico Superior de la cuenca lusitánica y comparación con el registro sincrónico de saurópodos de otras cuencas sedimentarias de la península ibérica.
- Estudio sistemático de los hallazgos recientemente publicados o inéditos atribuibles a saurópodos del Jurásico Superior portugués y comparación con el registro sincrónico previamente conocido para la península ibérica y para el área peri-atlántica.
- Análisis filogenético de los saurópodos del Jurásico Superior portugués incluyendo todos los taxones definidos para este período en la península ibérica y propuesta de una hipótesis de relación de parentesco que involucre a los taxones del Jurásico Superior europeo, norteamericano y africano.

Tanto la hipótesis general como estos objetivos están subordinados al desarrollo de distintas hipótesis y objetivos específicos.

Hipótesis 1.a. *Lourinhasaurus alenquerensis* es una forma exclusiva del Jurásico Superior portugués. Hipótesis 1.b. *Lourinhasaurus alenquerensis* es un miembro de Camarasauridae. Hipótesis 1.c. *Lourinhasaurus alenquerensis* está estrechamente relacionado con el género *Camarasaurus*.	Objetivo 1.a. Comprobar la validez de *Lourinhasaurus alenquerensis* y proponer una diagnosis revisada. Objetivo 1.b. Proponer una hipótesis de relación de parentesco para el lectotipo de *Lourinhasaurus alenquerensis*. Objetivo 1.c. Análisis sistemático del material clásico asignado a *Lourinhasaurus alenquerensis* de distintos yacimientos distribuidos en la localidades de São Bernardino, Areia Branca, Porto das Barcas, Salir de Matos, Alcobaça, Praia de Santa Cruz, Chiqueda de Cima, Vale Frades, Foz do Arelho, São Mamede, Torres Vedras y Ourém (Jurásico Superior, cuenca lusitánica).
Hipótesis 2.a. *Lusotitan atalaiensis* es una forma exclusiva del Jurásico Superior portugués. Hipótesis 2.b. *Lusotitan atalaiensis* es un miembro de Brachiosauridae	Objetivo 2.a. Comprobar la validez de *Lusotitan atalaiensis* y proponer una diagnosis revisada. Objetivo 2.b. Proponer una hipótesis de relación de parentesco para el holotipo de *Lusotitan atalaiensis*. Objetivo 2.c. Análisis sistemático del material clásico referido a *Lusotitan atalaiensis*, proveniente de las localidades de Areia Branca, Porto Novo (Maceira), Alcobaça, Cambelas y Praia das Almoinhas? (Jurásico Superior, cuenca lusitánica).

Hipótesis 3.a. *Dinheirosaurus lourinhanensis* es una forma exclusiva del Jurásico Superior portugués. Hipótesis 3.b. *Dinheirosaurus lourinhanensis* es un miembro de Diplodocinae.	Objetivo 3.a. Comprobar la validez de *Dinheirosaurus lourinhanensis* y proponer una diagnosis revisada. Objetivo 3.b. Proponer una hipótesis de relación de parentesco para el material tipo de *Dinheirosaurus lourinhanensis*.
Hipótesis 4.a. *Zby atlanticus* es una forma exclusiva del Jurásico Superior portugués. Hipótesis 4.b. *Zby atlanticus* es un miembro de Turiasauria.	Objetivo 4.a. Comprobar la validez de *Zby atlanticus* y propuesta de una diagnosis revisada. Objetivo 4.b. Proponer una hipótesis de relación de parentesco para el material tipo de *Zby atlanticus*.
Hipótesis 5. El ejemplar SHN 181, recogido en Valmitão (Lourinhã), no pertenece a ninguna de las especies previamente descritas, representando un nuevo taxón.	Objetivo 5. Estudio sistemático de SHN 181, un nuevo espécimen proveniente de los sedimentos de la Formación Praia de Amoreira-Porto Novo y recogido en Valmitão (Lourinhã).
Hipótesis 6.a. La diversidad de saurópodos presentes en la cuenca lusitánica se compone de turiasaurios, diplodócidos, camarasáuridos y braquiosáuridos. Hipótesis 6.b. La diversidad de saurópodos presente en la cuenca lusitánica se distribuye estratigráfica y geográficamente de forma homogénea a lo largo de toda la cuenca.	Objetivo 6.a. Obtener un contexto filogenético que integre, en una filogenia global, todos los taxones descritos en el Jurásico Superior portugués y evaluar la paleobiodiversidad del grupo en la cuenca lusitánica. Objetivo 6.b. Estudio sistemático de los dientes de saurópodo "en forma de corazón", "en forma de espátula", "en forma cono-cincel comprimido" y "en forma de cincel" de la cuenca lusitánica y análisis de su emplazamiento estratigráfico. Objetivo 6.c. Estudio sistemático de otro material craneal, axial y apendicular asignable a saurópodos hallado en niveles del Jurásico Superior de la cuenca lusitánica (sub-cuencas de Bombarral, Turcifal y Arruda) y análisis de su emplazamiento estratigráfico.
Hipótesis 7. La fauna de saurópodos del Jurásico Superior portugués está compuesta por formas distintas de aquellas presentes en el Jurásico Superior-Cretácico basal de España.	Objetivo 7. Comparar el registro del Jurásico Superior portugués y del Jurásico Superior-Cretácico basal español y establecer el grado de parentesco de cada uno de estos taxones entre sí y con los identificados en otros territorios.
Hipótesis 8. La relación de parentesco de los saurópodos del Jurásico Superior portugués con las faunas norteamericanas sincrónicas no soporta la presencia del contacto faunístico para ese momento, contrariamente a la hipótesis propuesta por otros autores con base en otros grupos faunísticos.	Objetivo 8. Comparar el registro del Jurásico Superior ibérico y norteamericano y establecer su grado de parentesco.

CHAPTER 3

Materials and methodology

3.1. MATERIALS AND METHODOLOGY

3.1.1. Materials

In order to drive the systematic study of the Portuguese Upper Jurassic sauropods the available bibliography was consulted, as well as, the direct observation of several specimens was performed resulting in detailed descriptions and documentation. This study included the type material of the established Portuguese taxa: *Lourinhasaurus alenquerensis*, *Dinheirosaurus lourinhanensis*, *Lusotitan atalaiensis* and *Zby atlanticus* (Lapparent and Zbyszewski, 1957; Dantas et al., 1998; Bonaparte and Mateus, 1999; Antunes and Mateus, 2003; Mateus et al., 2014). The studied sauropod specimens from the Portuguese Upper Jurassic record includes both several classical and other unpublished specimens found before the beginning of the present thesis, as well as specimens extracted in recent field work. Some researchers such as Pedro Dantas and José Luis Sanz supported the present research providing information and photographic record of several specimens. The present study is only focused on sauropod body fossils, being excluded any ichnological information related with sauropods.

Several paleontological collections with Portuguese Upper Jurassic sauropods were accessed. The classical material referred by Sauvage (1897-98), Zbyszewski (1946) and Lapparent and Zbyszewski (1957) is housed in Museu Geológico (Lisboa, Portugal), Museu Nacional de História Natural e da Ciência (Lisboa, Portugal), Museu Décio Thadeu do Instituto Superior Técnico (Lisboa, Portugal) and Museu Municipal Leonel Trindade (Torres Vedras, Portugal). Nevertheless, several new specimens found in the beginning of the twentieth century remains unpublished and many specimens have been discovered in the last 30 years. This material is mainly deposited in the following institutions: Museu Geológico (Lisboa, Portugal), Departamento de Geologia da Faculdade de Ciências da Universidade de Lisboa (Lisboa, Portugal), Museu Nacional de História Natural e da Ciência (Lisboa, Portugal), Sociedade de História Natural (Torres Vedras, Portugal), Museu da Lourinhã (Lourinhã, Portugal), Museu Municipal do Bombarral (Bombarral, Portugal), Museu Municipal de Porto de Mós (Porto de Mós, Portugal), Museu Municipal do Cadaval (Cadaval, Portugal) and Muséum national d'Histoire naturelle (Paris, France).

The study of Portuguese Upper Jurassic sauropods was complemented with a comparative study of other Iberian sauropods, and their incorporation in a new morphological data matrix. The studied and consulted specimens are deposited in Fundación Conjunto Paleontológico de Teruel-Dinópolis/Museo Aragonés de Paleontología (Teruel, Spain), Museo Nacional de Ciencias Naturales (Madrid, Spain), Museo de Ciencias Naturales (Valencia, Spain), Museo Provincial de Teruel (Teruel, Spain), Museo Paleontológico de Galve (Galve, Spain), Universidad Autónoma de Madrid (Madrid, Spain), Museo de las Ciencias de Castilla la Mancha (Cuenca, Spain), Museo Paleontológico de Alpuente (Alpuente, Spain), Museo de Ciencias Naturales de Álava (Vitoria, Spain) and Museo de Valltorta (Castellón, Spain).

In addition, several published (including type specimens) and unpublished specimens were analysed in order to incorporate information in our phylogenetic analyses. The accessed material is deposited in Natural History Museum of Los Angeles County (Los Angeles, USA), Muséum national d'Histoire naturelle (Paris, France), Humboldt Museum für Naturkunde (Berlin, Germany), Dinosaurier Freilichtmuseum Münchehagen/Verein zur Förderung der Niedersächsischen Paläontologie (Münchehagen, Germany), Natural History Museum (London, UK), Oxford University Natural History Museum (Oxford, UK), New Walk Museum (Leicester, UK) and Staatliches Naturhistorisches Museum (Braunschweig, Germany). Some material from the Middle Jurassic of Niger, temporally deposited on the Museo Paleontológico de Elche (Elche, Spain), was studied and incorporated in the present study.

3.1.2. Methodology

This thesis is composed by a set of manuscripts focused on the study of several sauropod specimen found in the Upper Jurassic sediments of the Lusitanian Basin. The present PhD dissertation tries to provide more information and improve the knowledge about the evolutionary history of this group of dinosaurs in this territory. Several manuscripts are based on the systematic revision of the classical material (chapter, 5, 10, 11) as well as, several unpublished specimens including material recovered in recent fieldworks (chapter 6-9, 12). The present PhD dissertation also provides a new phylogenetic context for *Dinheirosaurus lourinhanensis* and *Zby atlanticus*. No detailed descriptions for the latter taxa are presented, because they were recently published by other authors (Mannion et al., 2012; Mateus et al., 2014).

The terminology applied in the anatomical description of the vertebrae laminae and fossae follows Wilson (1999, 2012) and Wilson et al. (2011), respectively. The nomenclature applied in the descriptions of bones also follows Wilson and Sereno (1998). We use anterior and posterior ("romerian" nomenclature) instead cranial and caudal, generally used for the description in birds osteology (with the exception of the chapter 10). The position of caudal vertebrae in the tail followed Díez-Díaz et al. (2013), Mannion et al. (2013) and Tschopp et al. (2015). Herein, we prefer the term caudal rib instead transverse process (following Wilson, 2012).

In order to proceed to the phylogenetic study of the Upper Jurassic sauropods of the Lusitanian Basin (Portugal) we used the datasets of Wilson (2002), Upchurch et al. (2004), D'Emic (2012) and Carballido and Sander (2014). Several modifications were incorporated in these datasets and they will be explained in the respective chapters (10, 11 and 12). A new dataset incorporating all taxa from the Iberian Upper Jurassic is analyzed. This dataset is composed by 464 characters and 95 taxonomic units. Several characters incorporated in this dataset were previously proposed by Salgado et al. (1997), Wilson and Sereno (1998), Wilson (2002), Upchurch et al. (2004), Curry Rogers (2005), González Riga et al. (2009), Whitlock (2011), Santucci and Arruda-Campos (2011), Zaher et al. (2011), D'Emic (2012), Carballido et al. (2012), Mannion et al. (2012, 2013) and Tschopp et al. (2015). Some of the herein used characters are new or modified.

The used datasets were analyzed using TNT 1.1 (Goloboff et al., 2003) to find the most parsimonious trees (MPTs). The specific procedure for each analysis is explained in the chapters where phylogenetic analyses were performed. In chapter 10, some constrained analyses were carried out in TNT 1.1, to compare with previous phylogenetic approaches. The resulting MPTs were exported to PAUP 4.10b (Swofford, 2002) to run Templeton's tests of the unconstrained and constrained topologies.

3.2. MATERIALES Y METODOLOGÍA

3.2.1. Materiales

Para desarrollar el estudio sistemático de los saurópodos del Jurásico Superior portugués se ha realizado el análisis crítico de la información bibliográfica disponible, así como la observación directa, estudio y descripción de numerosos especímenes. Este conjunto de especímenes incluye el material tipo de los taxones portugueses hasta ahora establecidos: *Lourinhasaurus alenquerensis*, *Dinheirosaurus lourinhanensis*, *Lusotitan atalaiensis* y *Zby atlanticus* (Lapparent y Zbyszewski, 1957; Dantas et al., 1998; Bonaparte y Mateus, 1999; Antunes y Mateus, 2003; Mateus et al., 2014). En el conjunto de especímenes portugueses estudiados se incluye, además del material clásico, abundante material inédito, hallado tanto con anterioridad al comienzo de esta tesis doctoral, como recolectado en recientes campañas de excavación. Algunos investigadores, como es el caso de Pedro Dantas y José Luís Sanz, han facilitado documentación fotográfica detallada

de ejemplares concretos. El presente estudio se centra exclusivamente en el registro directo de saurópodos, no teniendo en cuenta aquel correspondiente a huellas y huevos asignados a este grupo.

Se han analizado varias colecciones paleontológicas de cara a estudiar los saurópodos del Jurásico Superior portugués. El material clásico de saurópodos portugueses publicado mayoritariamente por Sauvage (1897-98), Zbyszewski (1946) y Lapparent y Zbyszewski (1957) se encuentra depositado en las colecciones paleontológicas del Museu Geológico (Lisboa, Portugal), Museu Nacional de História Natural e da Ciência (Lisboa, Portugal), Museu Décio Thadeu do Instituto Superior Técnico (Lisboa, Portugal) y Museu Municipal Leonel Trindade (Torres Vedras, Portugal). Abundante material inédito hallado a principios del siglo XX y ejemplares recolectados en las últimas décadas del siglo XX y a principios del siglo XIX forman parte de las colecciones paleontológicas del Museu Geológico (Lisboa, Portugal), Departamento de Geologia da Faculdade de Ciências da Universidade de Lisboa (Lisboa, Portugal), Museu Nacional de História Natural e da Ciência (Lisboa, Portugal), Sociedade de História Natural (Torres Vedras, Portugal), Museu da Lourinhã (Lourinhã, Portugal), Museu Municipal do Bombarral (Bombarral, Portugal), Museu Municipal de Porto de Mós (Porto de Mós, Portugal), Museu Municipal do Cadaval (Cadaval, Portugal) y Muséum national d'Histoire naturelle (Paris, Francia).

El estudio de los saurópodos del Jurásico Superior portugués se ha completado con el análisis de otros ejemplares de saurópodos ibéricos, depositados en la Fundación Conjunto Paleontológico de Teruel-Dinópolis/Museo Aragonés de Paleontología (Teruel, España), Museo Nacional de Ciencias Naturales (Madrid, España), Museo de Ciencias Naturales (Valencia, España), Museo Provincial de Teruel (Teruel, España), Museo Paleontológico de Galve (Galve, España), Universidad Autónoma de Madrid (Madrid, España), Museo de las Ciencias de Castilla la Mancha (Cuenca, España), Museo Paleontológico de Alpuente (Alpuente, España), Museo de Ciencias Naturales de Álava (Vitoria, España) y Museo de la Valltorta (Castellón, España).

Además del material ibérico, varios especímenes publicados (incluyendo material tipo) e inéditos han sido analizados en las siguientes instituciones: Natural History Museum of Los Angeles County (Los Angeles, Estados Unidos), Muséum national d'Histoire naturelle (Paris, Francia), Humboldt Museum für Naturkunde (Berlín, Alemania), Dinosaurier Freilichtmuseum Münchehagen/Verein zur Förderung der Niedersächsischen Paläontologie (Münchehagen, Alemania), Natural History Museum (London, Reino Unido), Oxford University Natural History Museum (Oxforf, Reino Unido), New Walk Museum (Leicester, Reino Unido) y Staatliches Naturhistorisches Museum (Braunschweig, Alemania). Material procedente del Jurásico de Niger, depositado temporalmente en el Museo Paleontológico de Elche (Elche, España), ha sido también analizado.

3.2.2. Metodología

Con el objetivo de estudiar la historia evolutiva de los saurópodos portugueses, la presente memoria de tesis está compuesta por un compendio de varios trabajos enfocados en el estudio de material recolectado en la Cuenca Lusitánica. Estos trabajos incluyen tanto el estudio material clásico (capítulos 5, 10, 11), como ejemplares procedentes de excavaciones posteriores, correspondiendo, en su mayoría, a ejemplares hasta ahora inéditos (capítulos 6-9, 12). Aunque en esta memoria de tesis también se evalúa el contexto filogenético de *Dinheirosaurus lourinhanensis* y *Zby atlanticus*, no se presenta una descripción detallada de los mismos, puesto que ha sido recientemente efectuada por otros autores (Mannion et al., 2012; Mateus et al., 2014).

La terminología aplicada en la descripción anatómica de las láminas y fosas vertebrales se basan, respectivamente, en las propuestas nomenclaturales de Wilson (1999, 2012) y Wilson et al. (2011). La nomenclatura aplicada en descripción de los elementos óseos sigue aquella empleada

por Wilson y Sereno (1998). El uso de anterior y posterior (nomenclatura "romeriana") es empleado en lugar de craneal y caudal, generalmente utilizado en la descripción de la osteología de aves (con la excepción de capítulo 10). El posicionamiento de las vértebras caudales en serie caudal sigue los trabajos de Díez-Díaz et al. (2013), Mannion et al. (2013) y Tschopp et al. (2015). Tal como sugirió Wilson (2012), el término costilla caudal es empleado en lugar de proceso transverso.

Para proceder al estudio filogenético de los saurópodos del Jurásico Superior de la Cuenca Lusitánica (Portugal) se partió del empleo de las matrices de caracteres propuestas por Wilson (2002), Upchurch et al. (2004), D'Emic (2012) y Carballido y Sander (2014). Las modificaciones incorporadas en cada una de esas bases de datos serán expuestas en la explicación detallada de análisis aquí realizados (capítulos 10, 11 y12). Con el fin de integrar todos los taxones del Jurásico Superior portugués, se ha elaborado una única matriz de datos morfológicos, compuesta por 464 caracteres y 95 unidades taxonómicas. Varios de los caracteres utilizados están basados en caracteres morfológicos propuestos previamente por Salgado et al. (1997), Wilson y Sereno (1998), Wilson (2002), Upchurch et al. (2004), Curry Rogers (2005), González Riga et al. (2009), Whitlock (2011), Santucci y Arruda-Campos (2011), Zaher et al. (2011), D'Emic (2012), Carballido et al. (2012), Mannion et al. (2012, 2013) y Tschopp et al. (2015). Otros caracteres presentes en la matriz son nuevos, o están modificados de caracteres previamente propuestos por diversos autores.

La matriz resultante ha sido analizada mediante el empleo del programa TNT 1.1 (Goloboff et al., 2003), con el objetivo de obtener los árboles más parsimoniosos (MPTs). Los procedimientos específicos de cada uno de los análisis efectuados en esta tesis serán explicados en cada capítulo. Los valores para evaluar la robustez de los análisis (Bremer y Bootstrap) fueron también obtenidos mediante TNT 1.1. Con el objetivo de comparar determinadas topologías obtenidas en TNT 1.1 (capítulo 10) se han realizado varios análisis de Templeton con el programa PAUP 4.10b (Swofford, 2002),

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CHAPTER 4

Stratigraphic distribution of sauropod fossil record in the Portuguese Upper Jurassic of Lusitanian Basin

Stratigraphic distribution of the Upper Jurassic sauropod record in the Lusitanian Basin (Portugal)

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4.1. INTRODUCTION

The Upper Jurassic sediments of the Lusitanian Basin (Portugal) are known by abundant occurrences in fossil vertebrates, in particular dinosaurs, turtles and crocodyliforms (e.g. Sauvage, 1897-98; Lapparent and Zbyszewski, 1957; Dantas, 1990; Antunes and Mateus, 2003; Ortega et al., 2009, 2013). The sauropod fossil record is particularly rich in this basin, with several classical references (e.g. Sauvage, 1897-98; Lapparent and Zbyszewski, 1957). Four taxa, so far exclusive, were described: the camarasaurid *Lourinhasaurus alenquerensis* (Lapparent and Zbyszewski, 1957; Dantas et al., 1998; Mocho et al., 2014); the diplodocid *Dinheirosaurus lourinhanensis* (Bonaparte and Mateus, 1999; Mannion et al., 2012; recently also proposed as *Supersaurus lourinhanensis* by Tschopp et al., 2015), the basal macronaria and a putative brachiosaurid *Lusotitan atalaiensis*, (Lapparent and Zbyszewski, 1957; Antunes and Mateus, 2003; Mannion et al., 2013) and the turiasaur *Zby atlanticus* (Mateus et al., 2014).

The systematic revision of the some Portuguese Upper Jurassic taxa was recently performed (for *Dinheirosaurus* and *Lusotitan* see Mannion et al., 2012; 2013; for *Lourinhasaurus*, see Mocho et al., 2013a, 2014a). In addition, several new occurrences have been reported (Antunes and Mateus, 2003; Mateus, 2005, 2009; Royo-Torres et al., 2006, 2009; Yagüe et al., 2006; Ortega et al., 2010; Mannion et al., 2012, Mocho et al., 2012, 2013b, c, 2014b; Mateus et al., 2014). This new information shows a more diverse scenario for the sauropod faunas during the Upper Jurassic of the Lusitanian Basin than previously considered, with the identification of a clade previously unidentified in this basin, i.e., the basal eusauropod group Turiasauria. Royo-Torres et al. (2006) suggested the identification of Turiasauria in the Portuguese Upper Jurassic, and this point was posteriorly corroborated by the presence of new teeth and postcranial material (Mateus, 2009; Royo-Torres et al., 2009; Ortega et al., 2010; Mocho et al., 2012, in press). Mateus et al. (2014) defined a new turiasaur genus and species, *Zby atlanticus*, collected in the Vale de Pombas locality. This specimen was firstly related to *Camarasaurus* (Mateus, 2005) and posteriorly to *Turiasaurus riodevensis* (Mateus, 2009). *Zby* is considered as a member of the Turiasauria (Mateus et al., 2014) according the presence of several affinities with other members of this clade (Mateus, 2009; Mocho et al., 2012; Royo-Torres and Upchurch, 2012; Mateus et al., 2014).

The relationship between the Portuguese Upper Jurassic and North American Morrison Formation dinosaur faunas has been largely discussed. The relative abundant Portuguese vertebrate fossil record still remains important to understand the relationships between North American and European faunas in this period. A combination of shared and exclusive taxa was used as an argument to justify processes of dispersion or vicariance (Galton, 1980; Pérez-Moreno et al., 1999; Antunes and Mateus, 2003; Escaso et al., 2007; Ortega et al., 2013). The supposed close relationship of the Portuguese sauropods with taxa from the North American Upper Jurassic Morrison Fm. (e.g. Lapparent and Zbyszewski, 1957) is considered at the moment as less close than it is interpreted in other dinosaur groups (Galton, 1980; Pérez-Moreno et al., 1999; Mateus and Antunes, 2003; Malafaia et al., 2007, 2010, 2015; Hendrickx and Mateus, 2014), plants (Mohr, 1989), mammals (Martin, 2000), and ostracods (Schudack, 2000) with amphiatlantic distribution.

The present study provides a stratigraphic context for the Portuguese Upper Jurassic sauropods from the Lusitanian Basin, considering several geological areas such as the Bombarral (Bombarral-Alcobaça and Consolação), Turcifal and Arruda Sub-basins. Many specimens are reported and figured herein for the first time, including several specimens found in Torres Vedras, Lourinhã, Peniche, Caldas da Rainha and Pombal. Several specimens are under preparation but a preliminary systematic evaluation is done. This study aims to provide information about the composition of the sauropod faunas along the Upper Jurassic of the Lusitanian Basin and to evaluate if putative paleoecological constraints justify the distribution of the clades here indicated.

4.2. ANATOMICAL ABBREVIATIONS

aacet, articulation for the acetabulum; acc, acromial crest; acet, acetabulum; ant. spdl, anterior spinodiapophyseal lamina; asp, ascending process; aspa, articular surface for the ascending process; awf, apical wear facet; bi, bifurcation; br, bridge; cc, cnemial crest; cml, camellae; cpol, centropostzygapophyseal lamina; cr, caudal rib; cwf, carina wear facet; di, diapophyses; dpc, deltopectoral crest; ec, epicondyle; f, fossa; fic, fibular condyle; ft, fourth trochanter; gl, glenoid; gr, groove; ibi, incipient bifurcation; ilped, iliac peduncle; isped, ischiatic peduncle; lag, labial groove; lb, lateral bulge; lf, lingual facets; lic, lingual crest; lt, lateral trochanter; hy, hyposphene; lat.spol, lateral spinopostzygapophyseal lamina; of, obturator foramen; pafc, posterior astragalar fossa crest; paf, posterior astragalar fossa; pcdl, posterior centrodiapophyseal lamina; pcpl, posterior centroparapophyseal lamina; pl, pleurocoel; podl, postzygodiapophyseal lamina; posl, postspinal lamina; post. spdl, posterior spinodiapophyseal lamina; poz, postzygapophyses; prsl, prespinal lamina; prdl, prezygodiapophyseal lamina; prz, prezygapophyses; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprf, spinoprezygapophyseal fossa; sprl, spinoprezygapophyseal lamina; tap, triangular aliform process; tb, tuberosity; tia, tibial articular surface; tic, tibial condyle; vh, ventral hollow; vlc, ventrolateral crest; vpr, ventral process.

4.3. INSTITUTIONAL ABBREVIATIONS

MG, Museu Geológico, Lisboa, Portugal; ML, Museu da Lourinhã, Lourinhã, Portugal; MMPM, Museu Municipal de Porto de Mós, Porto de Mós, Portugal; MMB, Museu Municipal do Bombarral, Bombarral, Portugal; MMLT, Museu Municipal de Leonel Trindade, Torres Vedras, Portugal; MNHNC, Museu Nacional de História Natural e da Ciência, Lisboa, Portugal; SHN, Sociedade de História Natural, Torres Vedras, Portugal [plus (JJS) for the José Joaquim dos Santos collection deposited in the Sociedade de História Natural].

4.4. GEOLOGICAL CONTEXT

The Lusitanian Basin is an internal and intracratonic basin located on the west region of the Iberian Peninsula. This N-S elongated basin has a maximum extension of 225 km x 70 km (Kullberg, 2000). It is integrated by a set of marginal and peri-North Atlantic basins, which begin to be differentiated in the Triassic due the Pangea fragmentation, and, more specifically, to the North Atlantic opening (Ribeiro et al., 1979; Boillot et al., 1978; Kullberg et al., 2006, 2010). The Lusitanian Basin sedimentary sequence was deposited from the Middle Triassic (Ladinian? - Carnian) (Rocha et al., 1996) to the Lower Cretaceous (upper Aptian) (Rey, 1999). The evolution of this basin mainly occurs in a distensive tectonic context (Kullberg et al., 2006). In some regions, this sedimentary sequence reaches a thickness of 5000 meters (Ribeiro et al., 1979). This basin was divided in three main sectors by Rocha and Soares (1984).

The Upper Jurassic sequence in the Lusitanian Basin ranges from the middle Oxfordian to the boundary with the Lower Cretaceous (Schneider et al. 2009, see Fig. 4.1). It represents a third rifting episode (Rasmussen et al., 1998; Kullberg et al., 2006), marked by an internal differentiation, which resulted in the formation of several sub-basins (i.e. Turcifal, Arruda and Bombarral Sub-basins, Fig. 4.2a), located in the Central Sector of the Lusitanian Basin. This episode of rifting was followed by an important siliciclastic input, which progressively filled these sub-basins (Guéry, 1984; Hill, 1988; Wilson, 1988; Pena dos Reis et al., 2000; Kullberg et al., 2006, 2010). Since the Kimmeridgian up to the top of the Upper Jurassic, the sedimentary sequence was marked by a strong siliciclastic nature, with a continental signature (e.g. Hill, 1988, Manuppella et al., 1999; Kullberg et al., 2006). In this part of the sequence, the fossil record of terrestrial vertebrates is particularly rich (e.g. Lapparent and Zbyszewski, 1957; Dantas, 1992;

Antunes and Mateus, 2005; Ortega et al., 2009). The stratigraphy of the Upper Jurassic sequence of the Lusitanian Basin is complex, due the proposal of several stratigraphic approaches, and considering the profuse lateral heterogeneity (e.g. Hill, 1988; Leinfelder, 1993; Manuppella et al., 1999; Kullberg et al., 2006; Schneider et al., 2009; Martinius and Gowland, 2011; Taylor et al., 2013).

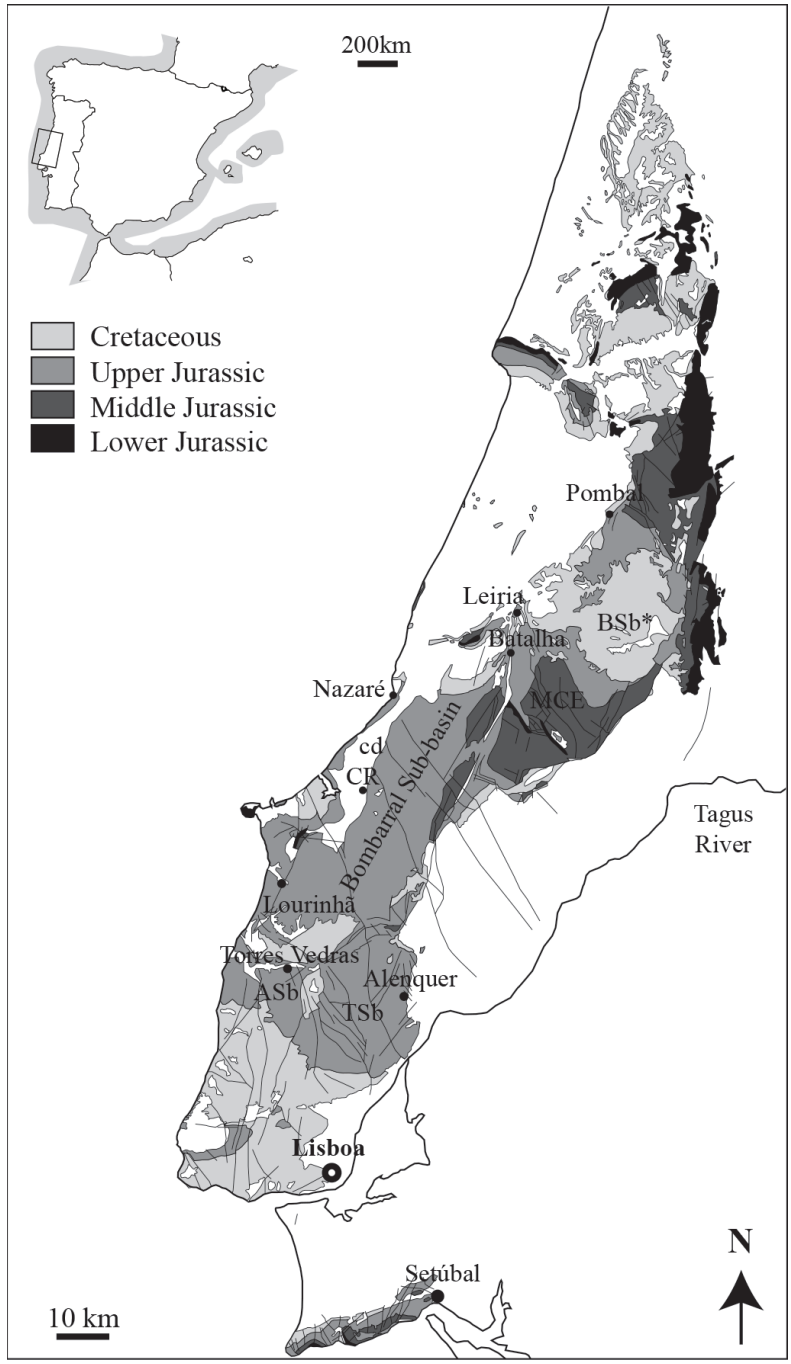

Figure 4.1. Geological map (adapted from Oliveira et al., 1992) showing the Portuguese Mesozoic levels outcropping in the Lusitanian Basin. ASb- Arruda Sub-basin; BSb – Bombarral Sub-basin, cd – Caldas Diapir; CR – Caldas da Rainha town; TSb – Turcifal Sub-basin.

4.5. UPPER JURASSIC SAUROPOD RECORD OF THE LUSITANIAN BASIN

4.5.1. Bombarral Sub-basin

The Bombarral Sub-basin corresponds to the widest Upper Jurassic sub-basin of the Central Sector of the Lusitanian Basin. It is also the richer area in fossil-sites with vertebrates (see Lapparent and Zbyszewski, 1957; Ortega et al., 2009). This basin is delimited on the north by the Nazaré Fault and on the east and south by Porto-Tomar, Arrife and Torres-Vedras-Montejunto Faults (Kullberg, 2000; Kullberg et al., 2006, 2010; Fig. 4.2a). The Torres Vedras-Montejunto Fault separates the Bombarral Sub-basin from the half-graben Turcifal and Arruda Sub-basins (Kullberg et al., 2006, 2010). Taylor et al. (2013) established two new sub-basins replacing the Bombarral Sub-Basin, called Consolação and Bombarral-Alcobaça Sub-basins (Fig.4.2b).

The Consolação Sub-basin is located on the west of the Lourinhã Fault and the Caldas Diapir, and is bounded on the north by the Nazaré Fault (Fig. 4.2b). This sub-basin includes the Upper Jurassic coastal sector from Praia da Consolação (Peniche) to Santa Cruz (Torres Vedras), and some Upper Jurassic cliffs outcropping north of Peniche and from Nazaré to Foz do Arelho. The remaining area of the previously defined Bombarral Sub-basin, and that on the east of the Lourinhã Fault and the Caldas Diapir, is now included in the Bombarral-Alcobaça Sub-basin (Fig. 4.2b, Taylor et al., 2013). Herein, we follow the sub-division of the Lusitanian Basin Central Sector proposed by Kullberg et al. (2006, 2010) always referring the correspondent nomenclature proposed by Taylor et al. (2013).

On the Bombarral Sub-basin several dinosaur occurrences have been reported since the end of the nineteenth century (e.g. Sauvage, 1897-98; Lapparent and Zbyszewski, 1957; Dantas, 1990; Antunes and Mateus, 2003), highlighting those on the Upper Jurassic sediments outcropping on Lourinhã, Peniche and Pombal municipalities (e.g. Lapparent and Zbyszewski, 1957; Pérez-Moreno et al., 1999; Antunes and Mateus, 2003). Several occurrences related to non-sauropod dinosaurs (theropods, ornithopods and theryophoreans) were also reported. Theropod faunas are composed by basal forms related to Ceratosauria (*Ceratosaurus* sp.), Megalosauroidea (*Torvosaurus gurneyi*) and Allosauroidea, such as *Allosaurus* and *Lourinhanosaurus antunesi* (e.g. Dantas, 1987; Dantas et al., 1999; Pérez-Moreno et al., 1999; Mateus et al., 1997; Mateus, 1998, 2005, 2006; Mateus and Antunes, 2000a, b; Rauhut, 2000; Mateus et al., 2006; Malafaia et al., 2007, 2008, 2010, 2015; Hendrickx and Mateus, 2012, 2014). More derived theropods are represented mostly by isolated specimens related to the clade Coelurosauria, including *Aviatyrannis*, indeterminate dromeosaurids, and a tooth attributed to cf. *Archaeopteryx* (Zinke and Rauhut, 1994; Antunes and Mateus, 2003; Zinke, 1998; Mateus, 2005; Malafaia et al., 2007, 2010, 2015). The most important Bombarral Sub-basin theropod fossil-sites are reported from Andrés in Pombal (Dantas et al., 1999; Pérez-Moreno et al., 1999; Malafaia et al., 2007, 2010), Paimogo in Lourinhã (Dantas, 1987; Mateus et al., 1997), Vale de Pombas-Praia Vermelha coastal cliffs in Lourinhã-Peniche (Mateus, 2005; Hendrickx and Mateus, 2014), and Guimarota mine in Leiria (Rauhut, 2000).

The Bombarral Sub-basin is also rich in ornithischian remains, highlighting the presence of at least four ornithopod and three thyreophoran forms. Several classical specimens were related to the genus *Omasaurus* (Zbyszewski, 1946; Lapparent and Zbyszewski, 1957), but part of this material, as well as new specimens, were posteriorly assigned to the genus *Dacentrurus* (e.g. Galton, 1991; Maidment et al., 2008; Ortega et al., 2009). This genus is also present in the Spanish Villar del Arzobisbo Formation (Tithonian-Berriasian in age), being the only known shared dinosaur genus between these territories for the Upper Jurassic (Cobos et al., 2010; Cobos and Gascó, 2013). More recently, two other stegosaurian forms were identified in the Upper Jurassic levels of the Bombarral Sub-basin. Escaso et al. (2007) related a partial individual found in Casal Novo

(Alcobaça Fm., Leiria) to the North American Morrison Fm. genus *Stegosaurus*, proposing an Upper Jurassic contact for the Iberian and North American faunas. Mateus et al. (2009) established a new stegosaurian taxon, *Miragaia longicollum*, a form close related to the *Dacentrurus*.

The ornithopod record of the Upper Jurassic Bombarral Sub-basin is represent by the dryosaurid *Eousdryosaurus* (Escaso et al., 2014) and two styracosternan: *Uteodon aphanoecetes*, previously identified in the Morrison Formation (Escaso et al., 2010a, b) and the exclusive Portuguese form *Draconyx loureiroi* (Mateus and Antunes, 2001). Another ornithopod based on teeth from the Guimarota mine was described as *Phyllodon henkeli* (Thulborn, 1973).

Other vertebrate groups have been reported, such as fishes (Sauvage, 1987-88; Kriwet, 2000; Balbino, 2003), amphibians (Wiechmann, 2000), turtles (Gassner, 2000; Pérez-García and Ortega, 2011; Pérez-García, 2015); sphenodonts (Malafaia et al., 2010), squamates (Broschinski, 2000; Caldwell et al., 2015), pterosaurs (Dantas, 1987; Wiechmann and Gloy, 2000), sphenodonts (Malafaia et al., 2010), crocodilyforms (Sauvage, 1897-98; Krebs and Schwarz, 2000; Schwarz and Salisbury, 2005; Tennant and Mannion, 2014), mammals (e.g. Hahn and Hahn, 2000; Krebs, 2000; Martin, 2000; Martin and Nowotny, 2000; Martin, 2005), and possible plesiosaurs (Castanhinha and Mateus, 2007).

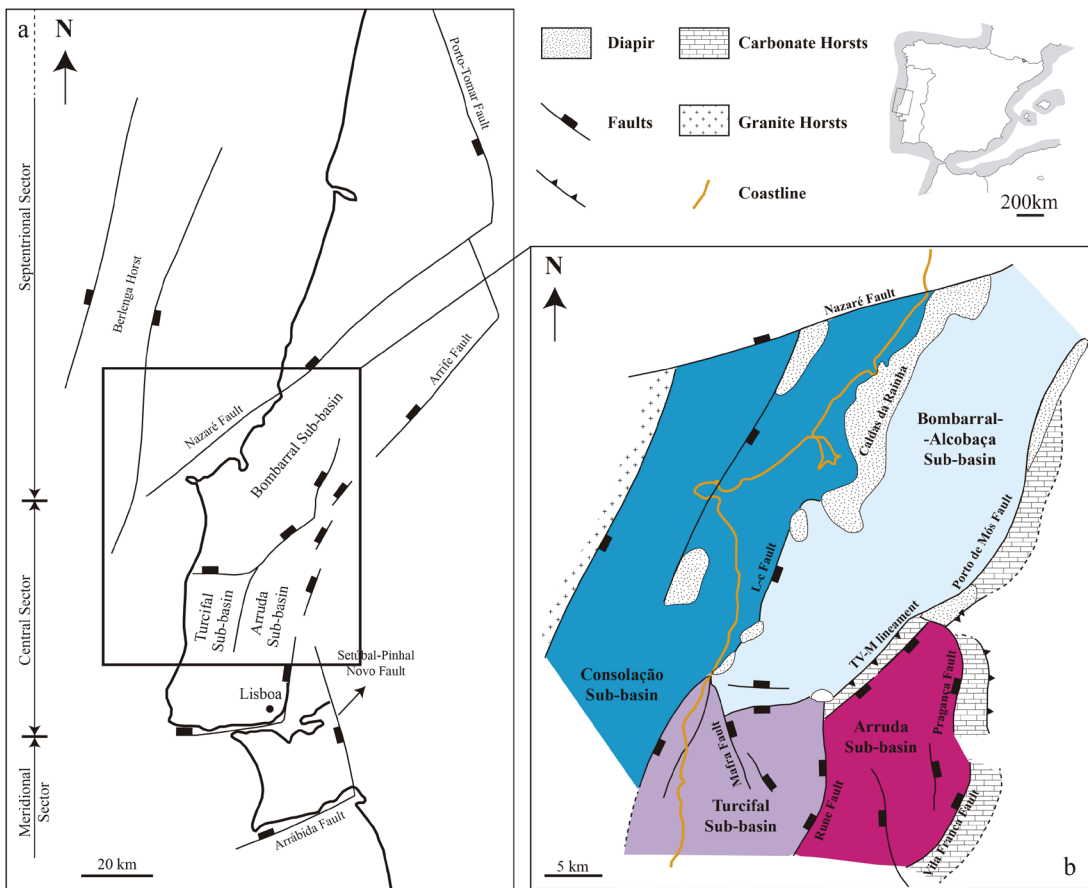

Figure 4.2. Lusitanian basin (divided in three sectors following Ribeiro et al., 1996) with the localization of the Upper Jurassic Sub-basins following two different interpretations: a) localization of Bombarral, Turcifal and Arruda Sub-basin (Guery, 1984; Kullberg, 2000; Kullberg et al., 2006; adapted from Kullberg, 2000; Alves, 2005; Kullberg et al., 2006); b) localization of Bombarral-Alcobaça, Consolação, Arruda and Turcufal Sub-basin (modified from Taylor et al., 2013).

The sauropods are well represented in this sub-basin, being recognized in many fossil-sites, with numerous occurrences (e.g. Lapparent and Zbyszewski, 1957; Dantas, 1990; Antunes and Mateus, 2003; Mateus, 2005; Mocho et al., 2013b, 2014b, 2015). Bellow, we will report the sauropod recorded in the different areas of the Bombarral Sub-basin.

North region of Maciço Calcário Estremenho (Figs. 4.3, 4.4): The region located North of the Maciço Calcário Estremenho (MCE) is rich in transitional to continental Upper Jurassic deposits (Camarate França and Zbyszewski, 1963; Teixeira et al., 1966; Manuppella et al., 2000), including several fossil sites in Pombal, Leiria, Batalha and Porto-de-Mós municipalities. Several important vertebrate sites are identified in this area, highlighting Guimarota mine (Leiria), Andrés (Pombal) and Casal Novo (Batalha) quarries (e.g. Pérez-Moreno et al., 1999; Rauhut, 2000; Escaso et al., 2007; Malafaia et al., 2007, 2010). The sauropod record is relatively poorly known in this sector of the Bombarral Sub-basin because is mainly based on incomplete specimens (Fig. 4.4). Samples come from sediments of the Alcobaça and Bombarral Formations (Figs. 4.3b-c, 4.4), including published and unpublished material (e.g. Malafaia et al., 2010). Herein, the Alcobaça Fm. is interpreted as deposited in marine environments transiting to fluvio-lacustrine deposits to the top of the Formation. In this area, the Alcobaça Fm. is lower Kimmeridgian-lower Tithonian in age, being considered as laterally correlated with the marine Abadia Fm., present on the south of the Lusitanian Basin Central Sector (Manuppella et al, 2000). Some important fossil-sites found in the Alcobaça Fm. correspond to fluvial (Escaso et al., 2007) and lagoon deposits (Schudack, 2000). The Bombarral Fm. is composed by fluvio-lacustrine deposits, dated as upper Kimmeridgian-Tithonian (Manuppella et al., 2000).

Close to the Pombal locality, sauropod fossils were only identified in the sediments of the Bombarral Formation. A great accumulation of fossils representing a relatively diverse vertebrate fauna was recognized at the Andrés locality in Tithonian levels of the Bombarral Fm. (Dantas et al., 1999; Pérez-Moreno et al., 1999; Malafaia et al., 2007, 2009, 2010). Several teeth and postcranial material assigned to Sauropoda were collected in this fossil-site (Fig. 4.4e). A preliminary analysis on the tooth material allowed to recognize four morphotypes: heart-, spatulate-, compressed cone-chisel-, and peg-shaped, suggesting the presence of forms related to Diplodocoidea, Turiasauria and Titanosauriformes (Malafaia et al., 2010). Nevertheless, more tooth and postcranial material is being prepared (pers. comm. EM).

Also in the Pombal area, a middle/posterior caudal vertebra (MG 4811, Fig. 4.4d) was found in Albergaria dos Doze (Pombal) probably from the Bombarral Formation (Fig. 4.3b). Lapparent and Zbyszewski (1957) attributed this element to the theropod *Megalosaurus pombali*. Subsequently, Mateus (2005) considered this vertebra as belonging to an indeterminate theropod. Nevertheless, this vertebra probably corresponds to an indeterminate sauropod based on its general morphology, the absence of ventral crest and an anteroposteriorly short neural arch. A middle or posterior dorsal neural spine was also found in this area, more precisely, next to Vermoil (Bombarral Fm., Fig. 4.4i-j). This unpublished specimen is housed in the paleontological collections of the Muséum national d'Histoire naturelle at Paris. This neural spine probably represents a eusauropod due the presence of a transversely expanded neural spine and the presence of well-defined prespinal laminae. More recently, a new fossil-site containing a partial sauropod skeleton (dorsal vertebrae and ribs) was found in Pombal (Fig. 4.4o), and it is being explored by the Museu Nacional de História Natural e da Ciência (Lisboa, Portugal).

A large area with Upper Jurassic continental sediments from the Alcobaça and Bombarral Formations is located in the localities of Batalha, Vila Nova de Ourém, Leiria and Porto-de-Mós. In Alcobaça Fm., one of the most important accumulations was found in the Guimarota mine, in Leiria (e.g. Rauhut, 2000). The Guimarota fossil record is relatively poor in sauropod remains, but some small teeth related to Brachiosauridae (Rauhut, 2000), or inclusively to cf. *Lusotitan atalaiensis* (Mateus, 2005) were found (Fig. 4.4b-c). Sauvage (1897-98) and Lapparent

and Zbyszewski (1957) also reported some localities with dinosaur occurrences near Vila Nova de Ourém and Porto de Mós (probably from Alcobaça Fm.). Two teeth, one of them with heart-shaped morphology probably related to Turiasauria (MG 16, Mocho et al., 2012, in press; Fig. 4.4f-h) and the other with compressed cone-chisel-shaped morphology common in Titanosauriformes (MG 125, Fig. 4.4a), were found near Ourém. An unpublished posterior caudal vertebra (MMPM.P/554) from an indeterminate sauropod was also found in Fonte do Oleiro (Alcobaça Fm.), south of Porto de Mós town.

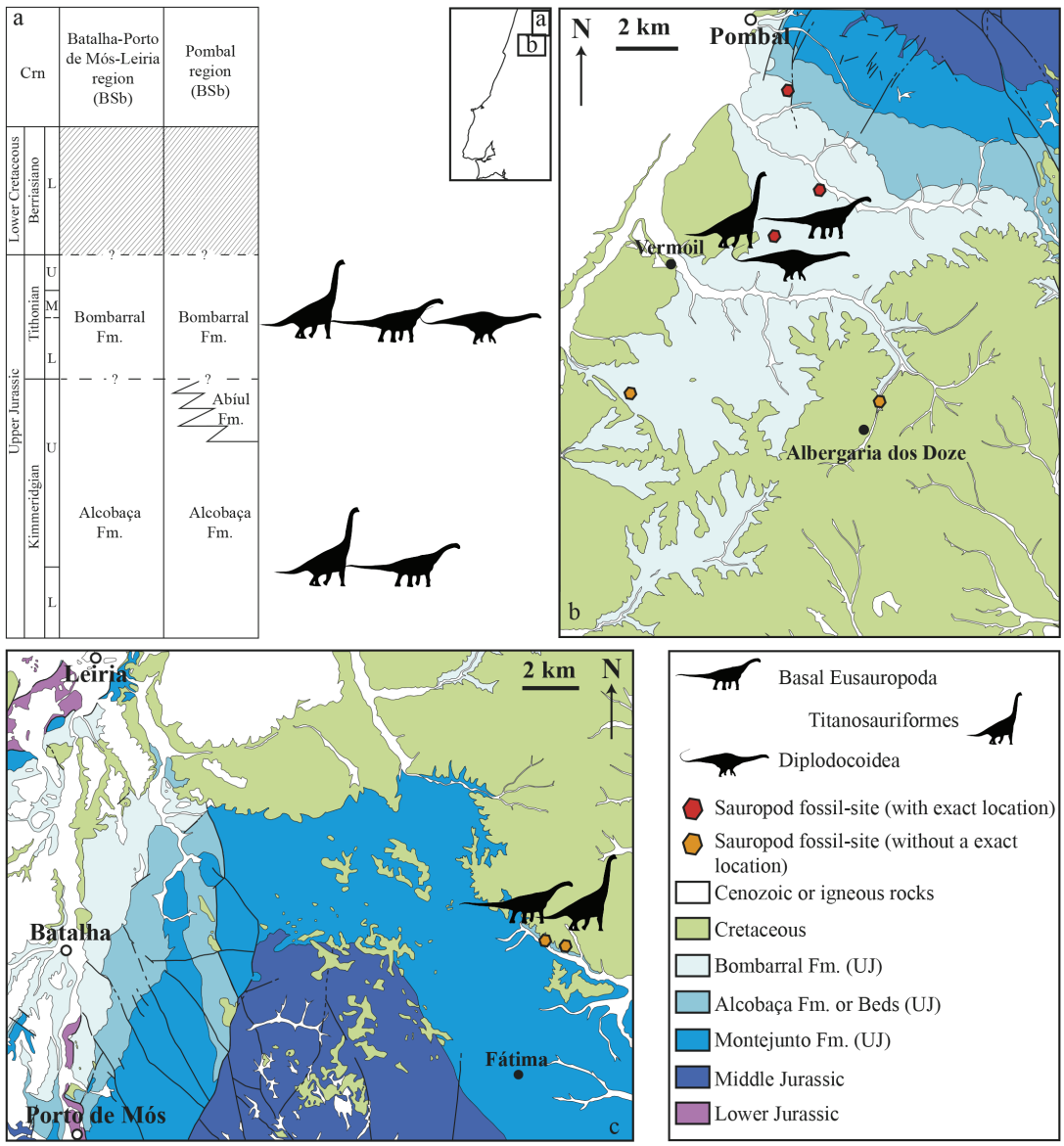

Figure 4.3. a) Simplified stratigraphy of the Kimmeridgian-Tithonian sequence in Pombal, Leiria and Batalha areas (Manuppella et al., 2000; Kullberg et al., 2006; Escaso et al., 2007; Malafaia et al., 2010) with distribution of main sauropod clades identified in this area. b-c) Geological map of Pombal (b) and Leiria and Batalha (c) areas with the localities yielding fossil remains referred to Sauropoda (modified from Teixeira et al., 1966; Zbyszewski et al., 1974; Zbyszewski and Ferreira, 1978; Manuppella et al., 2000). Crn – Chronostratigraphy.

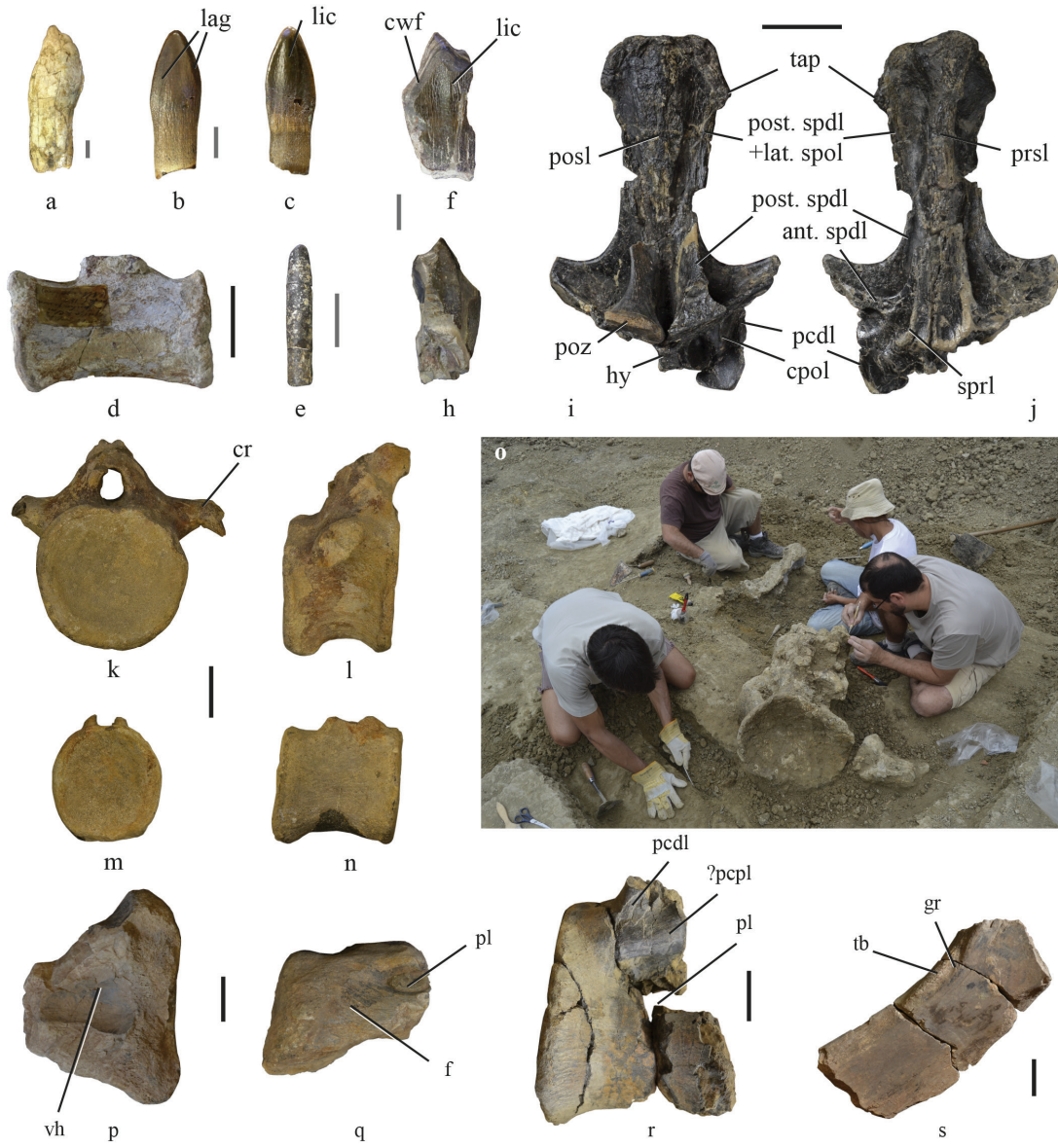

Figure 4.4. Cranial and postcranial sauropod remains from Pombal, Leiria and Batalha areas: a) Titanosauriformes indet., compressed cone-chisel-shaped tooth (MG 8779, Ourém) in labial view; b-c) Titanosauriformes indet., compressed cone-chisel-shaped tooth (MG 27891, Guimarota) in labial (b) and lingual (c) views; d) Sauropoda indet., middle or posterior caudal vertebra (MG 4811, Albergaria dos Doze) in right view; e) Diplodocoidea indet., pencil-shaped teeth (MNHNUL/AND.303, Andrés) in lingual view; f-h) ?Turiasauria indet., heart-shaped tooth (MG 16, Ourém) in labial (f) and lingual (h) views; i-j) Eusauropoda indet., posterior or middle dorsal neural spine (unlabeled, Vermoil) in posterior (i) and anterior (j) views; k-n) Sauropoda indet., anterior and middle caudal vertebra from a partial caudal series (MG 4974, Abadia) in posterior (k, m) and right (l, n) views; o) sauropod fossil-site in Junqueira locality (Pombal); p-s) sauropod material from near Batalha (MG 30389) that might represent an indeterminate diplodocine, middle caudal vertebra in ventral (p) and right (q) views, partial posterior (?) dorsal centrum in right view (r), and partial ischiatic peduncle in medial view (s). Black scale bar: 10 cm; Gray scale bar: 0.5cm. See Anatomical abbreviations for abbreviations.

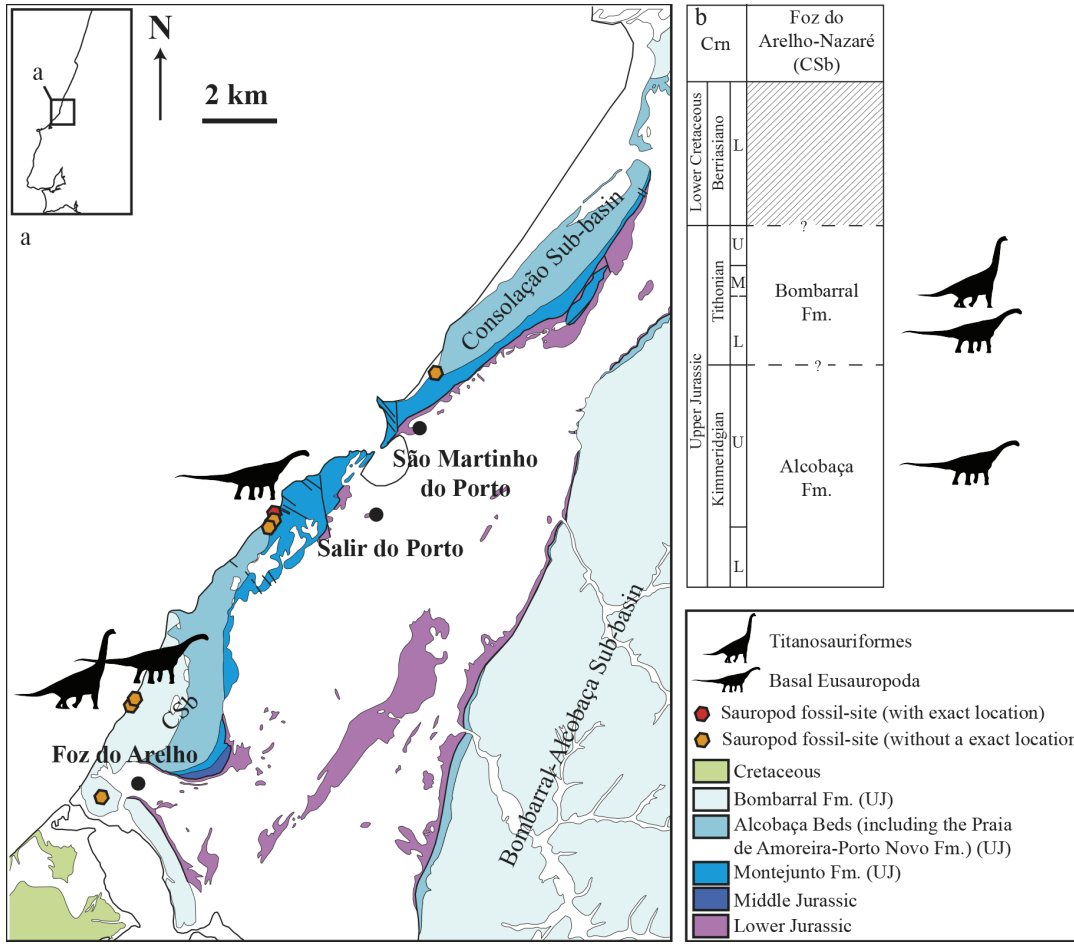

Figure 4.5. a) Geological map of the coastal sector of Foz do Arelho to Nazaré, and part of the Consolação Sub-basin following Taylor et al. (2013) (modified from Zbyszewski and Moitinho de Almeida, 1960; Camarate França and Zbyszewski, 1963; Azerêdo et al., 2010) area with the localities yielding fossil remains referred to Sauropoda. b) Simplified stratigraphy of the Kimmeridgian-Tithonian sequence for the coastal sector of Foz do Arelho to Nazaré sector based on Azerêdo et al. (2010) with the stratigraphic distribution of the main sauropod clades identified in this area. Crn – Chronostratigraphy.

Some unpublished specimens related to Sauropoda were found close to Batalha town and are deposited in the collections of the Museu Geológico and Museu Municipal de Porto-de-Mós, highlighting *i*) a partial dorsal centrum and a partial caudal series collected in Abadia (MG 4974, Fig. 4.4k-n), *ii*) and a set of sauropod bones including dorsal and caudal vertebrae and a fragmentary ischium from Batalha (MG 30389; Fig. 4.4p-s). The identified middle caudal vertebra (Fig. 4.4p-q) of the MG 30389 set shares the presence of a quadrangular cross-section, ventral hollow and lateral fossae with the members of Diplodocinae. The stratigraphic and geographic context of these specimens is not clear, and they might pertain to Alcobaça Fm. or Bombarral Fm.

Therefore, the presence of eusauropods, probably turiasaurs, indeterminate diplocoids (including members of Diplodocinae) and macronarians, possible brachiosaurids (based on tooth occurrences) is identified in the area located north of the Maciço Calcário Estremenho (Fig. 4.3a).

Coastal sector of Foz do Arelho to Nazaré (Figs. 4.5, 4.6): A wide sector with Upper Jurassic sediments on the Bombarral (following Kullberg et al., 2006, 2010; Azerêdo et al., 2010), or Consolação Sub-basin (following Taylor et al., 2013), is identified west of the Caldas Diapir (Fig. 4.5a). This sequence extends from the coastal cliffs from Foz do Arelho to Nazaré (e.g. Hill, 1988; Kullberg et al., 2006), and includes sediments of the Alcobaça (Kimmeridgian to basal Tithonian) and Bombarral (Tithonian) Formations (Kullberg et al., 2006, 2010; Schneider et al., 2009; Azerêdo et al., 2010). Both formations are particularly rich in fossil vertebrate occurrences. One of the most important fossil sites is the classical locality Murteiras (Caldas da Rainha) (Lapparent and Zbyszewski, 1957) due the presence of several specimens related to *Dacentrurus* (Galton, 1991; Antunes and Mateus, 2003; Maidment et al., 2008). Nevertheless, no sauropod remains were reported there (Lapparent and Zbyszewski, 1957).

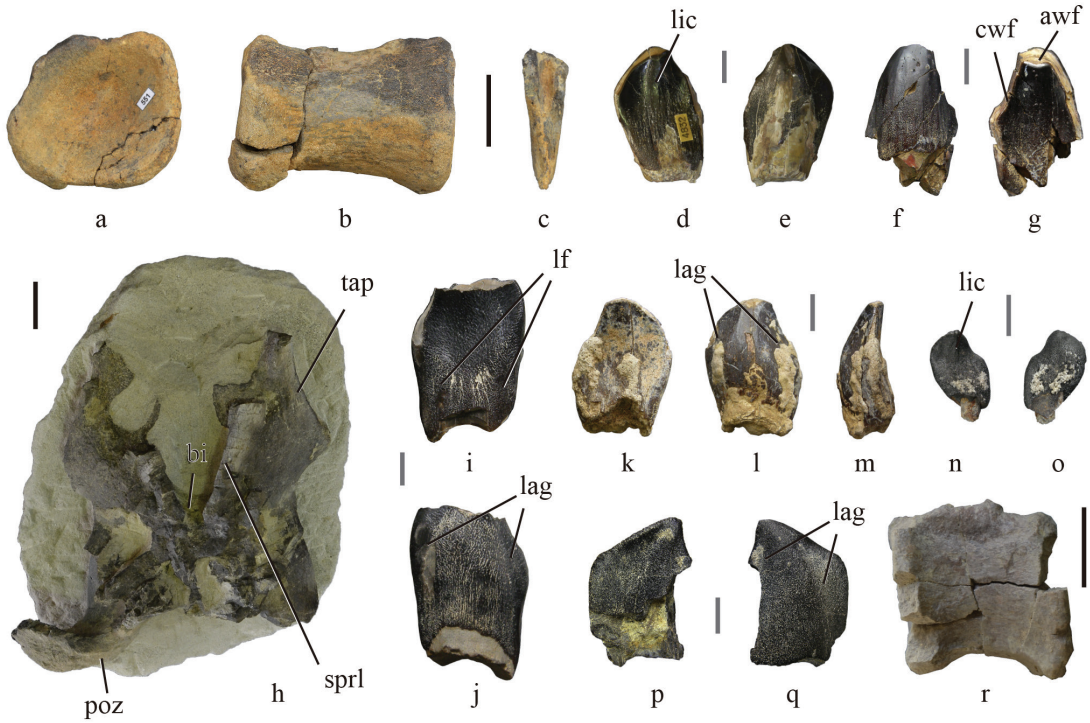

Figure 4.6. Cranial and postcranial sauropod remains from the coastal sector of Foz do Arelho to Nazaré: a-c) Eusauropod material (MMPM.P/551) found near São Martinho do Porto locality, middle caudal vertebra in posterior (a) and right (b) views and a partial anterior or middle chevron in posterior view (c); d-e) ?Turiasauria indet., heart-shaped tooth (MG 4832, São Martinho do Porto) in lingual (d) and labial (e) views; f-g) ?Turiasauria indet., heart-shaped tooth (SHN 501, Praia da Gralha) in labial (f) and lingual (g) views; j) Eusauropoda indet., partial posterior cervical or anterior dorsal neural arch (MG 4920, Foz do Arelho); i-j) Eusauropoda indet., spatulate-shaped tooth (SHN 517, Foz do Arelho) in lingual (i) and labial (j) views; k-m) ?Turiasauria indet., heart-shaped tooth (SHN 508, Serra do Bouro) in lingual (k), labial (l) and distal (m) views; n-o) ?Turiasauria indet., heart-shaped tooth (SHN 512, Foz do Arelho) in lingual (n) and labial (o) views; p-q) ?Turiasauria indet., heart-shaped tooth (SHN (JJS) 146, Salir do Porto) in lingual (p) and labial (q) views; r) Sauropoda indet., middle caudal vertebra (SHN 537, Salir do Porto) in left view. Black scale bar: 5 cm; Gray scale bar: 0.5cm. See Anatomical abbreviations for abbreviations.

Sauropod remains collected in the Alcobaça Formation (following Camarate França and Zbyszewski, 1963; Azerêdo et al., 2010) outcropping in this sector of the Bombarral Sub-basin (Fig. 4.5a) include unpublished axial elements (MMPM.P/551, Fig. 4.6a-c) found close to São Martinho do Porto, and some unpublished caudal vertebrae and pelvic fragments (SHN 537, Fig. 4.6r) found in Salir do Porto. A bifurcated posterior cervical or anterior dorsal neural spine (MG 4920, Lapparent and Zbyszewski, 1957; Fig. 4.6h) of an indeterminate eusauropod from Foz do Arelho (Caldas da Rainha) was collected in the sediments of the Bombarral Fm.

Several teeth were collected on this coastal area corresponding to several morphotypes: *i*) heart-shaped teeth (Fig. 4.6d-g, k-o, p-q), tentatively related with Turiasauria (Royo-Torres et al., 2009; Mocho et al., 2012, in press; Royo-Torres and Upchurch, 2012); *ii*) spatulate-shaped teeth (Fig. 4.6i-j; unpublished material housed in MG and SHN) related to an indeterminate eusauropod (probably a macronarian); and *iii*) compressed cone-chisel-shaped teeth (unpublished material housed in the SHN), related to the Titanosauriformes clade. The first of these morphotypes is recognized as the most abundant in this coastal sector.

The classical and the new occurrences show a relatively high potential for the study of the sauropods and other fossil clades of this area. However, the so far published (Mocho et al., 2012, 2015, in press) and unpublished material of sauropods only allow identify the presence of indeterminate sauropods and eusauropods, possible members of Turiasauria, and indeterminate titanosauriforms (attributions mainly based on tooth material) (Fig. 4.5b).

Alcobaça, Bombarral and A-dos-Cunhados (Figs. 4.7, 4.8): A large area with Upper Jurassic sediments, included on the Bombarral Sub-basin, is identified at the east of the Lourinhã Fault and the Caldas Diapir, considered as Bombarral-Alcobaça Sub-basin by Taylor et al. (2013) (Fig. 4.7a). This area was poorly prospected when compared with other areas as the coastal sector from Praia da Consolação to Torres Vedras. In fact, this area is mainly under soil resulting in only a few vertebrate occurrences, highlighting the localities of Moita dos Ferreiros (Mateus, 2005; Mannion et al., 2012), and Miragaia, where the type material of *Miragaia longicollum* was found (Mateus et al., 2008, 2009). In this area, scarce sauropod occurrences were referred (Fig. 4.7a), including some specimens housed in private collections (e.g. Mateus, 2005; pers. observ., PM), such as a partial tail of an indeterminate sauropod, collected close to the Bombarral town.

Some classical occurrences from the Alcobaça Formation were found in the Alcobaça, Bombarral and A-dos-Cunhados region (Bombarral-Alcobaça Sub-basin) and referred to Sauropoda (Lapparent and Zbyszewski, 1957): *i*) an heart-shaped tooth (Fig. 4.8f-g) from Fervença (Sauvage, 1897-98; Lapparent and Zbyszewski, 1957), tentatively related to an indeterminate eusauropod probably related to Turiasauria (Mocho et al., in press); and *ii*) a posterior caudal vertebra from Chiqueda de Cima (Lapparent and Zbyszewski, 1957), corresponding to an indeterminate sauropod. In the Bombarral Fm. sediments some elements were found: *i*) an anterior caudal vertebra (Fig. 4.8e, MG 4804) of an indeterminate eosauropod from Salir de Matos; *ii*) a middle caudal vertebrae (Fig. 4.8c-d, MG 4819, 4821, 4826) of an indeterminate diplodocine from São Gregório da Fanadia; and *iii*) A large left astragalus (Fig. 4.8a-b, MMPM.P/75), so far unpublished, was found in Imaginário (Caldas da Rainha).

An incomplete skeleton composed by axial elements (cervical and dorsal vertebrae; ML 418; Fig. 4.8h), considered aff. *Dinheirosaurus* (Antunes and Mateus, 2003) and *Apatosaurus* sp. (Mateus, 2005), was found Close to Moita dos Ferreiros (Lourinhã, Bombarral Formation). These bones are bad preserved, especially, the preserved cervical vertebra. Mannion et al. (2012) distinguished this specimen from *Dinheirosaurus lourinhanensis* and suggested that it might represent a second diplodocid taxon for the Upper Jurassic of the Lusitanian Basin. Tschopp et al. (2015) considered that it represents an indeterminate diplodocine different from *Dinheirosaurus*. The full preparation of the *Dinheirosaurus lourinhanensis* dorsal vertebrae will be important to test this hypothesis.

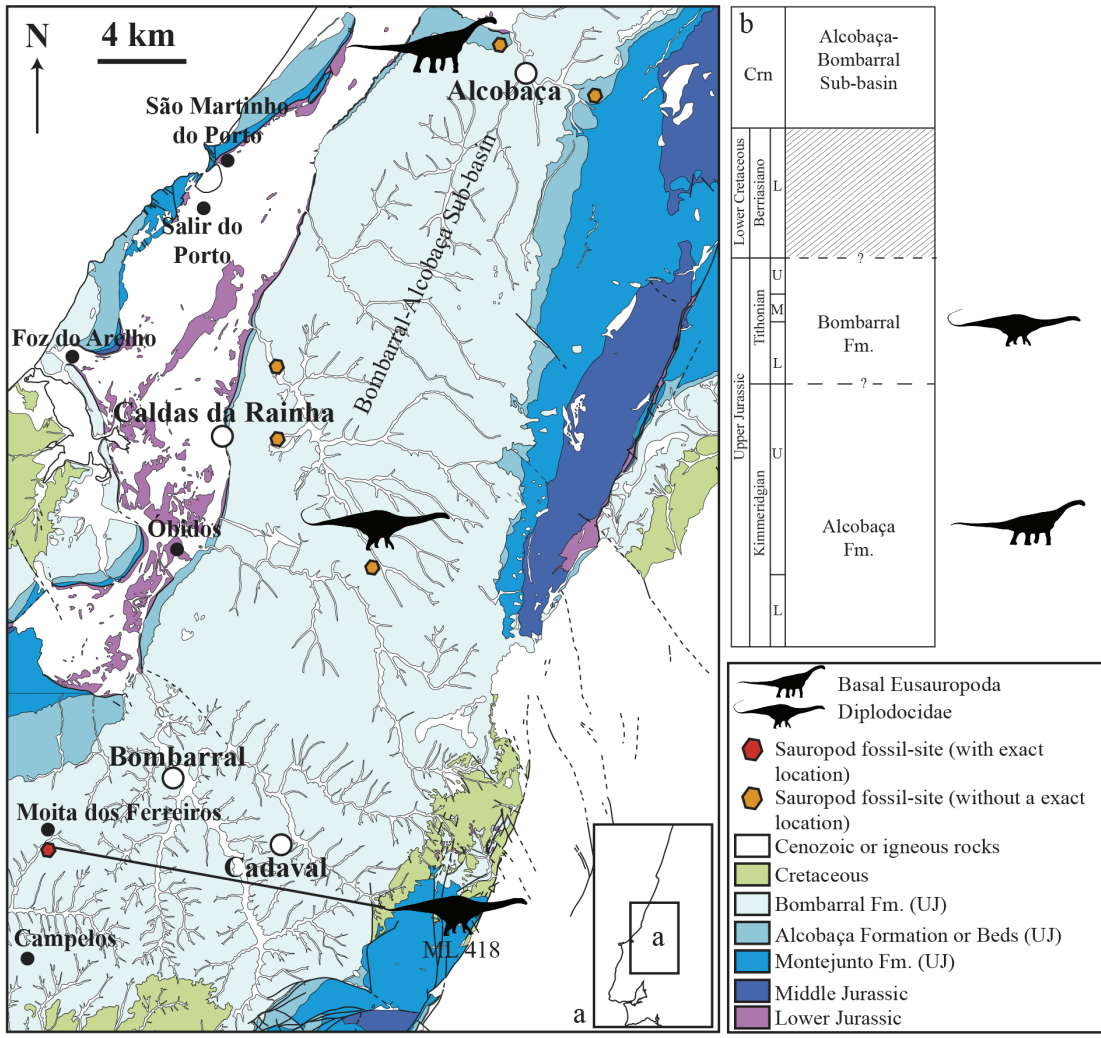

Figure 4.7. a) Geological map of the Bombarral-Alcobaça Sub-basin following Taylor et al. (2013) (modified from Camarate França et al., 1960; Zbyszewski and Moitinho de Almeida, 1960; Camarate França and Zbyszewski, 1963; Zbyszewski and Torre de Assunção, 1965; Zbyszewski et al., 1966, Azerêdo et al., 2010) area with the localities yielding fossil remains referred to Sauropoda. b) Simplified stratigraphy of the Kimmeridgian-Tithonian sequence for Bombarral-Alcobaça Sub-basin based on Azerêdo et al. (2010) with the stratigraphic distribution of the main sauropod clades identified in this area. Crn – Chronostratigraphy.

Summarizing, the dinosaur faunas in the Alcobaça-Bombarral-A-dos-Cunhados area are poorly understood. In this area, the recorded sauropod fauna is composed by indeterminate taxa, and indeterminate eusauropod (tentatively assigned to Turiasauria) and indeterminate diplodocines. One of the diplodocine specimens (ML 418) might represent a diplodocine different from *Dinheirosaurus lourinhanensis* (Mannion et al., 2012; Tschopp et al., 2015).

North Peniche (Figs. 4.9, 4.10): An Upper Jurassic section including the Praia de Amoreira-Porto Novo and Bombarral Formations, outcrops north of the Peniche town (Manuppella et al., 1999; Azerêdo et al, 2010) (Fig. 4.9). Some stratigraphic approaches suggested for the presence of the Sobral Fm. along this sequence (e.g. Hill, 1988; Martinius and Gowland, 2011) (Fig. 4.9b).

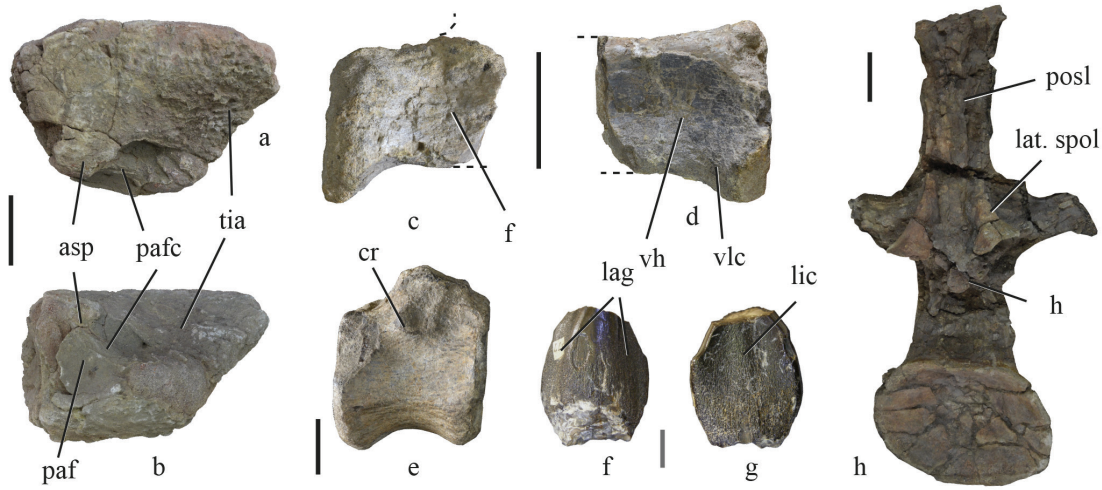

Figure 4.8. Cranial and postcranial sauropod remains from the Alcobaça, Bombarral and A-dos-Cunhados area: a-b) Eusauropoda indet., left astragalus (MMPM.P/75, Imaginário) in proximal (a) and posterior (b) views; c-d) Diplodocinae indet., middle caudal vertebra (MG 4819, São Gregório da Fanadia) in right (c) and ventral (d) views; e) Eosauropoda indet., anterior caudal vertebra (MG 4804, Salir de Matos) in right view; f-g) ?Turiasauria indet., heart-shaped tooth (MG 277, Fervença) in lingual (f) and labial (g) views; h) Diplodocinae indet., middle or posterior dorsal vertebra (ML 418, Moita dos Ferreiros) in posterior view. Black scale bar: 10 cm; Gray scale bar: 0.5cm. See Anatomical abbreviations for abbreviations.

This section is not very large (its maximum length is about 2 km), but is rich in fossil-sites, some of them known since the first half of the twentieth century. The most important dinosaur site is in Pedras Muitas (Peniche) where it has been collected remains of sauropods and stegosaurs (Zbyszewski, 1946; Lapparent and Zbyszewski, 1957). Its precise location is not clear. According to the available stratigraphic information (e.g. Lapparent and Zbyszewski, 1957; Camarate França et al., 1960; Hill, 1988; Bernardes, 1992; Schneider et al., 2009; Azerêdo et al., 2010; Martinius and Gowland, 2011; Taylor et al., 2013), these elements probably came from sediments of the Praia de Amoreira-Porto Novo Fm. Several partial middle and posterior cervical vertebrae, housed in the Museu Geológico, representing sauropods, compose the available set of fossils from Pedras Muitas. These remains include a misidentified cervical vertebra, previously considered as part of an *Omosaurus* individual (Zbyszewski, 1946, pl. I, fig. 1). This specimen includes a middle and posterior cervical vertebrae (Fig. 4.10e-f), which have being subject to a systematic revision.

Other sauropod remains were also identified to the north of Peniche. Most of these specimens are deposited in the collections of the MG, ML and SHN. A so far unpublished partial spatulate-shaped tooth (Fig. 4.10a, MG 8783), bearing lingual facets, was found in Baleal. It can be attributed to an indeterminate eusauropod, possible a basal macronarian. This tooth morphology is common in mamenchisaurids (Ouyang and Ye, 2002), basal macronarians (Osborn and Mook, 1921; Gilmore, 1925; Ostrom and McIntosh, 1966) and in the euhelopodid *Euhelopus* (Wilson and Upchurch, 2009). Heart-shaped teeth (Fig. 4.10b-c) are also reported on this area (Mocho et al., 2012, in press), which might indicate the presence of turiasaurian eusauropods on these sediments outcropping to the north of Peniche. The SHN houses several specimens from Baleal, Pedras Muitas and Almagreira (Fig. 4.9c) that still need preparation, including several axial and appendicular elements (e.g. Fig. 4.10h-j). One of those specimens is an anterior caudal vertebra with a slight procoelous centrum (Fig. 4.10i, SHN 180). The overall morphology (e.g. slight procoelous centrum and short neural spine with distal rugosities) resembles that an anterior caudal vertebrae collected on the Spanish sediments of the Villar

de Arzobispo Formation, in San Lorenzo (Riodeva), attributed by Cobos et al. (2011) to Turiasauria. The presence of procoelous condition is shared with several clades within the Eusauropoda clade (e.g. Wilson, 2002; Upchurch et al., 2004). Some compressed cone-chisel-shaped teeth (Fig. 4.10d, g) collected Baleal-Pedras Muitas coastal section are deposited in SHN collections. This tooth morphology has been considered as a feature of Titanosauriformes clade (Upchurch et al., 2004).

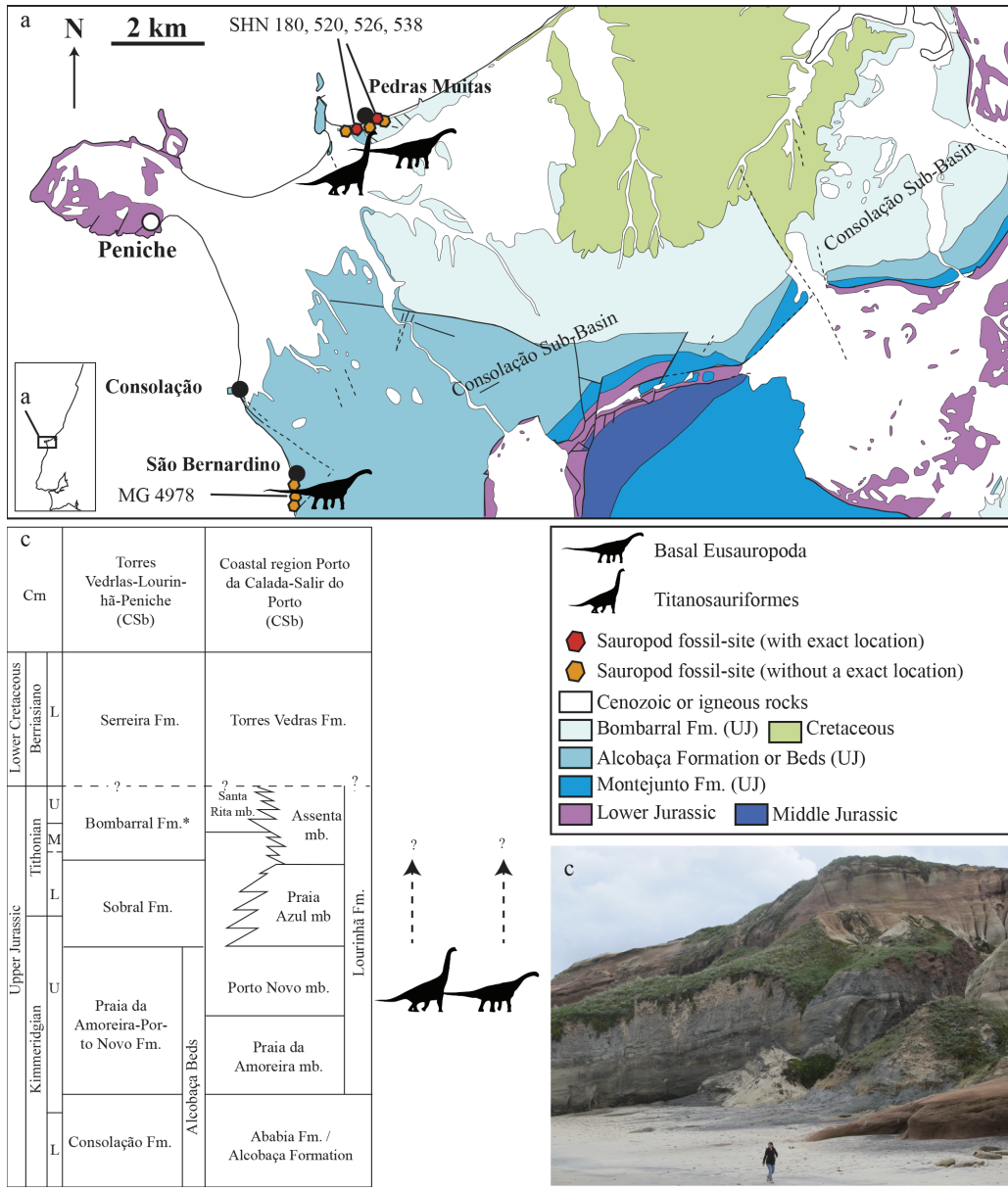

Figure 4.9. a) Geological map of the Peniche area incorporated in the Consolação Sub-basin following Taylor et al. (2013) (modified from Camarate França et al., 1960; Zbyszewski and Moitinho de Almeida, 1960; Azerêdo et al., 2010) with the localities yielding fossil remains referred to Sauropoda. b) Simplified stratigraphy of the Kimmeridgian-Tithonian sequence for Peniche area based on Manuppella et al. (1999, first column) and Hill (1988, second column) with the stratigraphic distribution of the main sauropod clades identified in this area. c) Sediments of the Bombarral Fm. in the Almagreira Cliffs. Crn – Chronostratigraphy

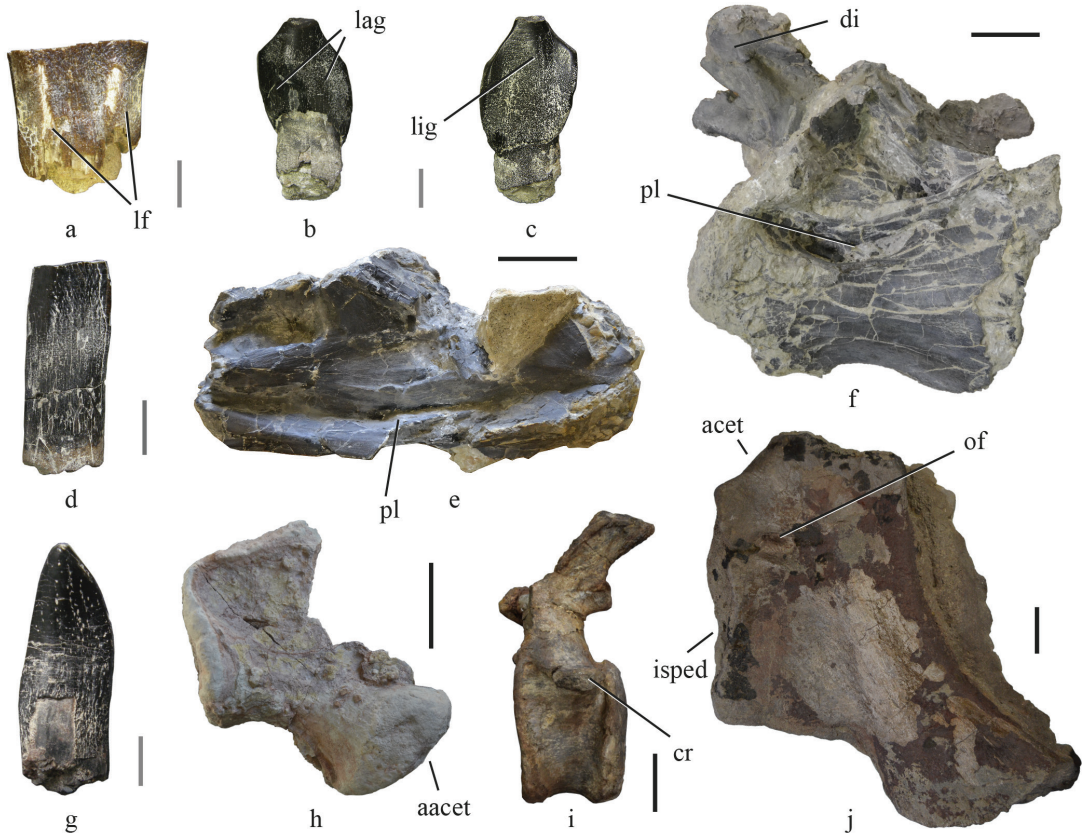

Figure 4.10. Cranial and postcranial sauropod remains from the cliffs located on North of Peniche (incorporated on Consolação Sub-basin following Taylor et al., 2013): a) Eusauropoda indet., partial spatulate-shaped tooth (MG 8783, Baleal) in lingual view; b-c) ?Turiasauria indet., heart-shaped tooth (SHN (JJS) 141, Baleal) in labial (b) and lingual (c) views; d) Titanosauriformes indet., compressed cone-chisel-shaped tooth (SHN 547, Pedras Muitas) in lingual view; e-f) Eusauropoda indet., middle (MG 4917) and posterior cervical vertebrae from Pedras Muitas in right (e) and left (f) views, respectively; g) Titanosauriformes indet., compressed cone-chisel-shaped tooth (SHN 543, Baleal) in lingual view; h) sacral rib (SHN, 538, Almagreira) in posterior or anterior view. i) Eusauropoda indet., anterior caudal vertebra (SHN 180, Baleal) in left view (i); j) Macronaria indet., right pubis (SHN 526, Almagreira) in lateral view. Black scale bar: 10 cm; Gray scale bar: 1 cm. See Anatomical abbreviations for abbreviations.

The detailed systematic study of the sauropods collected in the north of Peniche still needs to be performed. However, the so far available information allows to identify the presence both turiasaurians and basal macronarians (Fig. 4.9).

Praia da Consolação-Lourinhã-Torres Vedras coastal sector (Figs. 4.11-4.14): Praia da Consolação-Lourinhã-Torres Vedras coastal sector is the most rich area in the Lusitanian Basin concerning Upper Jurassic dinosaur remains (e.g. Lapparent and Zbyszewski, 1957; Dantas, 1990; Antunes and Mateus, 2003; Ortega et al., 2009, 2013) (Fig. 4.11a). A thick Upper Jurassic sedimentary sequence outcrops in this sector and includes deposits of the Praia de Amoreira-Porto Novo, Sobral and Bombarral Formations. This continental sedimentary sequence was deposited above the marine Abadia Fm. (Manuppella et al., 1999) (Fig. 4.11b). The type specimens of *Lusotitan atalaiensis*, *Dinheirosaurus lourinhanensis* and *Zby atlanticus* (Lapparent and

Zbyszewski, 1957; Dantas et al., 1992; Antunes and Mateus, 2003; Bonaparte and Mateus, 1999; Mannion et al., 2012, 2013; Mateus et al., 2014) were found in this area of the Bombarral Sub-basin (Consolação Sub-basin following Taylor et al., 2013). In addition, many of published and unpublished specimens, most of them housed in MG, ML and SHN paleontological collections, were also collected there (Bonaparte and Mateus, 1999; Mateus, 2005; Yaguë et al., 2006; Mannion et al., 2012; Mocho et al., 2013b, 2014b).

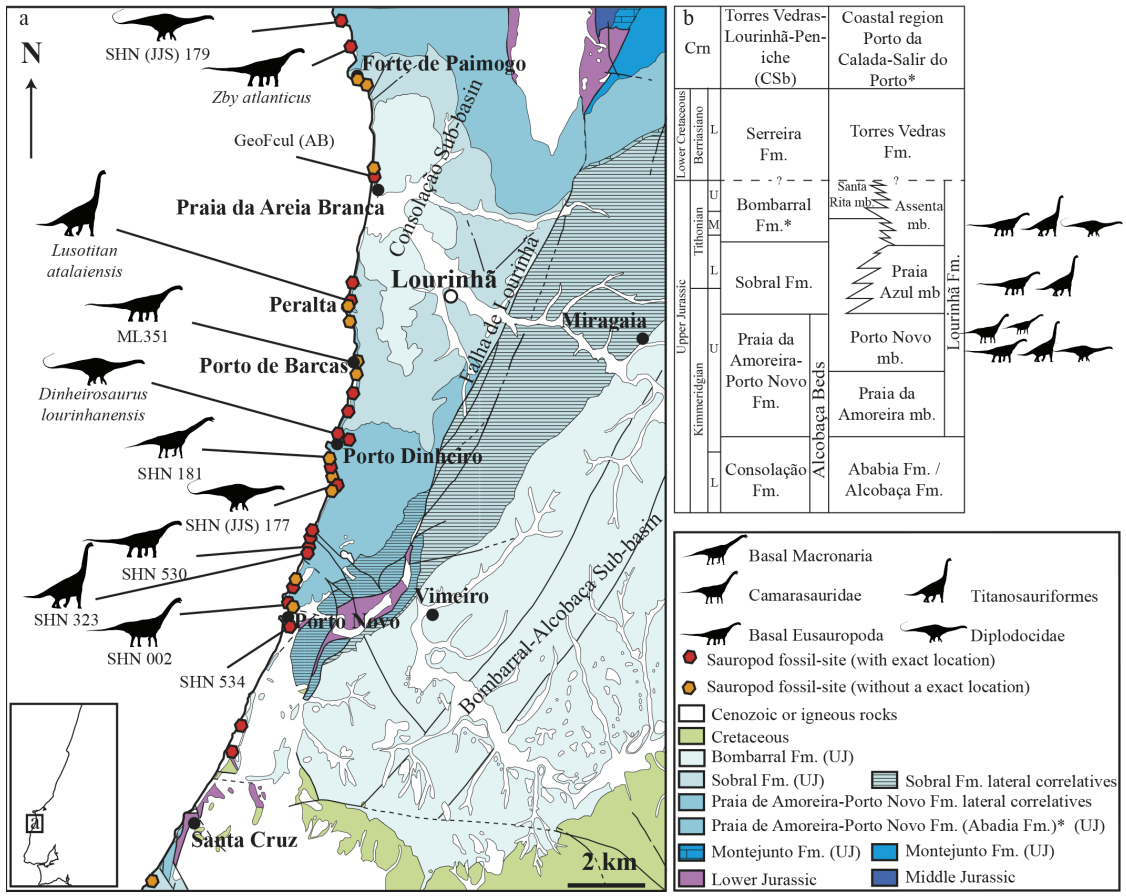

Figure 4.11. a) Geological map of the coastal sector of Praia da Consolação-Lourinhã-Torres Vedras (area incorporated in the Consolação Sub-basin following Taylor et al., 2013) (modified from Manuppella et al., 1999) with the localities yielding fossil remains referred to Sauropoda. b) Simplified stratigraphy of the Kimmeridgian-Tithonian sequence for the coastal sector of Peniche-Lourinhã-Torres Vedras based on Manuppella et al. (1999, first column) and Hill (1988, second column) with the stratigraphic distribution of the main sauropod clades identified in this area. Crn – Chronostratigraphy

The Praia de Amoreira-Porto Novo Formation outcrops in several points along this sector, highlighting the sedimentary sections from São Bernardino to Paimogo, and from Porto Dinheiro to Praia de Santa Rita (Hill, 1988; Manuppella et al., 1999; Mateus et al., 2013). This Upper Kimmeridgian-basal Tithonian formation (Fürsich, 1981; Manuppella et al., 1999) is well-known by its abundant dinosaur fossil remains, including several sauropod specimens (Lapparent and Zbyszewski, 1957; Manuppella et al., 1999; Dantas, 1990; Antunes and Mateus, 2003; Ortega et al., 2009). This formation is interpreted as deposited in a fluvial and meandriform to alluvial environment (Hill, 1988, 1989).


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The holotype of *Zby atlanticus* (Fig. 4.12m-p) was found in the Vale de Pombas cliffs (north of Forte de Paimogo), in the Praia de Amoreira-Porto Novo Formation. This partial skeleton includes a tooth, a chevron, a right partial scapula and coracoid, an almost complete right forelimb, and indeterminate elements (Mateus, 2005, 2009; Mateus et al., 2014; pers. observ. PM). The material of *Zby atlanticus* was firstly attributed to the North American Morrison genus *Camarasaurus* (Mateus, 2005), and posteriorly to *Turiasaurus riodevensis* (Mateus, 2009). Mateus et al. (2014) described the species *Zby atlanticus* as a member of Turiasauria. The affinities between *Zby* and the members of Turiasauria clade were previously discussed by other authors (Mateus, 2009; Mocho et al., 2012; Royo-Torres and Upchurch, 2012).

Lapparent and Zbyszewski (1957) referred the presence of some specimens collected north of the Forte de Paimogo (Praia de Amoreira-Porto Novo Formation). Non-sauropod dinosaurs were also found in this locality (Lapparent and Zbyszewski, 1957; Escaso et al., 2008; Hendrickx and Mateus, 2014). A partial caudal series (MG 4978), with 15 caudal vertebrae, was found in São Bernardino (Peniche). A partial right humerus (Fig.4.12y) of a sauropod was found in Praia dos Frades (Peniche). It was attributed to *Apatosaurus alenquerensis* (Lapparent and Zbyszewski, 1957). This humerus shares the presence of a crest in the posterior face of the humeral proximal end is identified here as a shared feature with the humerus of *Duriatitan humerocristatus*, from the British lower Kimmeridge Clay Fm. (Barrett et al., 2010), but just can be determined as an indeterminate eusauropod. An unpublished metacarpal I (SHN 583) found in Praia dos Frades (Peniche) shares the morphology of the metacarpal I in *Turiasaurus riodevensis* and *Zby atlanticus*. Therefore, it is tentatively considered as cf. Turiasauria.

There is available a so far unprepared diplodocid specimen (Fig. 4.12aa, SHN (JJS) 179) from Praia da Vermelha (Peniche, Praia de Amoreira-Porto Novo Formation), composed by axial and appendicular elements, that was recovered in Praia Vermelha (Peniche, Mocho et al., 2014b).

Figure 4.12. Cranial and postcranial sauropod remains from sediments of the Praia de Amoreira-Porto Novo Fm. of the coastal sector of Praia da Consolação-Lourinhã-Torres Vedras: a-b) ?Turiasauria indet., heart-shaped tooth (SHN (JJS) 142, Praia da Corva) in lingual (a) and labial (b) views; c-d) Eusauropoda indet., spatulate-shaped tooth (SHN 513, Porto Novo) in lingual (c) and labial (d) views; e-f) Titanosauriformes indet., compressed cone-chisel-shaped tooth (SHN 578, Valmitão) in lingual (e) and labial (f) views; g-h) Eusauropoda indet., partial left maxilla (SHN 582, Praia dos Frades) in lateral (g) and posterior (h) views; i) Titanosauriformes indet., posterior caudal vertebra (SHN 523, Praia da Corva) in right view; j-l) Diplodocinae indet., partial skeleton (SHN (JJS) 177, Valmitão), anterior caudal neural spine in posterior view (j), anterior caudal centrum in right view (k) and left ischium in medial view (l); m-p) holotype material of *Zby atlanticus* (ML 368, Vale de Pombas), right ungueal I in lateral view (m), right humerus in anterior view (n), right radius in posterior view (o), right ulna in lateral view (p); q) Eusauropoda indet., partial distal forked-chevron (SHN 587, Praia da Corva) in medial view; r) Sauropoda indet., pedal ungueal I (SHN 524, Praia de Pedrogãos) in lateral view; s-v) Macronarian indet., partial skeleton (SHN 181, Valmitão), right astragalus in proximal view (s), anterior caudal vertebra in anterior view (t), right tibia in lateral view (u) and right fibula in medial view (v); w-x) Eusauropoda indet., partial skeleton (SHN 530, Praia da Corva), anterior chevron in anterior view (w) and anterior caudal vertebra in posterior view (x); y) cf. *Duriatitan humerocristatus*, humerus (MG 4976, Praia dos Frades) in anterior view; z) Sauropoda indet., partial skeleton (SHN 534, Santa Rita), middle chevron in posterior view; aa) Diplodocidae indet., partial skeleton (SHN (JJS) 179, Praia Vermelha), dorsal/caudal (?) neural spine in posterior view; bb-dd) holotype material of *Dinheirosaurus lourinhanensis* (ML 414, Porto Dinheiro), proximal end of a dorsal rib in anterior view (bb), anterior caudal neural spine in posterior view (cc) and articulated dorsal vertebrae in lateral view (dd). Black scale bar: 10 cm; Gray scale bar: 5 cm; brown scale bar: 1 cm. See Anatomical abbreviations for abbreviations.

The morphology of the neural spines (posterior dorsal or anterior caudal), with a well-defined prespinal lamina, rectangular shape (anteroposteriorly compressed), and with a slight dorsal bifurcation, is similar to the exclusive morphology in the posterior dorsal and anterior caudal neural spines of diplodocids such as *Supersaurus*, *Dinheirosaurus*, *Diplodocus* and *Barosaurus* (e.g. Hatcher, 1901; Lull, 1919; McIntosh, 2005; Mannion et al., 2012; pers. observ., PM). Other unprepared sauropod specimens from this sector, and also belonging to the Praia de Amoreira-Porto Novo Fm., are housed in SHN and ML paleontological collections (see list of Mateus, 2005, for ML; pers. observ., PM). Several teeth have also been found between Forte de Paimogo and Praia da Consolação, being recognized heart-shaped teeth, probably related to Turiasauria (Mocho et al., 2012, in press); spatulate-shaped teeth (e.g. SHN 516, SHN 540), attributed to indeterminate eusauropods, probably basal macronarians; and compressed cone-chisel-shaped teeth (e.g. SHN 546), share the morphology of those of Titanosauriformes. A skull fragment bearing heart-shaped teeth was found in Praia dos Frades (Fig. 4.12g-h, SHN 582), probably from a turiasaurian sauropod.

South of Porto Dinheiro, the type locality of *Dinheirosaurus lourinhanensis* (Dantas et al., 1992; Bonaparte and Mateus, 1999; Mannion et al., 2012) outcrops an extensive section of the Praia de Amoreira-Porto Novo Formation. The border between the Torres Vedras and Lourinhã municipalities is located in this relatively poorly-prospected area. New discoveries reveal a rich dinosaur fauna, including theropods, ornithopods, thyreophorans and sauropods, as well as other vertebrate clades such as turtles and crocodilyforms (e.g. Malafaia et al., 2008; Escaso et al., 2010a, b; Pérez-García and Ortega, 2011). Several fossil sites containing sauropods were found in this area, including some partial skeletons.

Figure 4.13. a) *Dinheirosaurus lourinhanensis* dorsal series (ML 414) in Porto Dinheiro with the paleontologist Pedro Dantas during the year 1991. A partial skeleton in the field (SHN 534) collected in Santa Rita, including a partial tail (b) and several appendicular bones (c).

The first remains of the holotype of *Dinheirosaurus lourinhanensis* were identified in 1987, in the cliffs of Porto Dinheiro. Consequently, in 1988 and 1991, a team composed by members of the MNHNC (Lisboa, Portugal), Salamanca University (Salamanca, Spain) and GEAL (Lourinhã, Portugal) proceeded to the extraction of a series of partially articulated cervical and dorsal vertebrae, with associated dorsal ribs, as well as caudal vertebrae and pelvic elements (Figs. 4.12bb-dd, 4.13a) (Dantas et al., 1992). Bonaparte and Mateus (1999) defined a new diplodocid taxon, *Dinheirosaurus lourinhanensis*, being considered as a diplodocine form close related with the North American Upper Jurassic *Supersaurus* (Rauhut et al., 2005; Whitlock, 2011; Mannion et al., 2012; Tschopp and Mateus, 2013; Tschopp et al., 2015). In fact, Tschopp et al. (2015) suggested that *Dinheirosaurus lourinhanensis* could corresponds to a species of *Supersaurus*, proposing the new combination *Supersaurus lourinhanensis*. Several remains from the type specimen (ML 414), including several caudal vertebrae (pers. observ., FO and PM), needs to be prepared for the confirmation or refutation of this hypothesis. The *Dinheirosaurus* type locality is stratigraphically close to the boundary between the Praia de Amoreira-Porto Novo and the Sobral Formations (Manuppella et al., 1999; field observations).

Another partial diplodocid individual was found in Valmitão (Lourinhã), southern of Porto Dinheiro (Mocho et al., 2014b). This specimen and the *Dinheirosaurus* holotype are the most complete diplodocids of the European Upper Jurassic record. The Valmitão specimen (SHN (JJS) 177) is composed by axial elements (dorsal?, sacral and anterior caudal vertebrae; ribs and chevrons) and pelvic girdle bones (ilia, ischia and pubis) (Fig. 4.12j-l). SHN (JJS) 177 could be referred to Flagellicaudata by the presence of expanded distal end of the ischia (following Whitlock, 2011). Rectangular anterior caudal neural spines in the anterior view, and the presence of diapophyseal laminae on the anterior caudal ribs, support the assignation of SHN (JJS) 177 to Diplodocidae (sensu Whitlock, 2011). The wing-like caudal ribs morphology of the anterior caudal vertebrae, the presence of a dorsal concavity in the neural spines (slightly bifurcated), and the ventral and lateral pneumaticity, suggest that the SHN (JJS) 177 has a close relationship with diplodocines such as *Diplodocus* and *Barosaurus* (Hatcher, 1901; Osborn, 1904; Lull, 1919; McIntosh, 2005; Whitlock, 2011; Tschopp et al., 2015).

Many sauropod specimens coming from the coastal cliffs between Porto Dinheiro and Santa Rita are housed in the SHN, and most of them still needs preparation. Mateus (2005) also referred an appreciable number of specimens coming from this area, and deposited in the ML. In 2003 and 2009, the SHN proceeded to the excavation (Fig. 4.13b-c) in Santa Rita (Torres Vedras) of a partial articulated skeleton, including a partial tail and pelvis, associated with limb bones (Fig. 4.12z, SHN 534). The systematic context of this specimen still needs to be clarified. Next to this quarry is located the type locality of the pleurosternid turtle *Selenemys lusitanica*, also from the Praia de Amoreira-Porto Novo Formation (Pérez-García and Ortega, 2011). Other fossil site prospected by the SHN is located in Porto Novo (Torres Vedras). Several axial and appendicular bones were recovered there. This specimen (SHN 002) shares with the camarasaurid *Lourinhasaurus alenquerensis* the general morphology of the forelimb bones, nevertheless, no diagnostic can be identified. These two fossil-sites are stratigraphically close to the upper boundary of the Praia de Amoreira-Porto Novo Fm. with the Sobral Fm. (Manuppella et al., 1999; field observations). Another specimen (SHN 530), including sacral and caudal vertebrae, and appendicular bones (Fig. 4.12w-x), was found in the cliffs of Praia da Corva (Torres Vedras). The caudal vertebrae (Fig. 4.12x) resemble the morphology present in Iberian turiasaurs, being marked by the presence of slight procoelous anterior caudal vertebrae. This specimen also preserves long and bridged anterior chevrons, as occur in some basal eusauropods such as *Spinophorosaurus* (pers. observ., PM). Also from Praia da Corva, an unpublished set of anterior, middle and posterior caudal vertebrae (Fig. 4.12i) probably belonging to a single individual was found (SHN 523). It might represents an indeterminate titanosauriform based on the presence of anteriorly displaced neural

arch, lateral fossae, and dorsoventrally compressed centrum. Finally, a medium size individual (SHN 181) found in Valmitão, also unpublished, is being prepared and described. It includes caudal vertebrae, and pectoral, pelvic and hindlimb elements (Fig. 4.12s-v). This specimen presents several peculiar features and probably corresponds to a new sauropod taxon. Also, several tooth with different morphotypes have been recovered between Porto Dinheiro and Santa Rita. These specimens include heart-shaped (Fig. 4.12a-b, see Mocho et al., 2012, in press), spatulate-shaped (Fig. 4.12c-d, SHN 513), and compressed cone-chisel-shaped teeth (Fig. 4.12e-f, SHN 574, 575, 578).

The Sobral Formation is laterally correlative to the lowest part of the Bombarral Fm., representing a regional transgression. The Sobral Fm. was deposited in a marginal marine to deltaic environment (Hill, 1988; Manuppella et al., 1999). In the west part of the Bombarral Sub-basin (i.e. Consolação Sub-basin following Taylor et al., 2013), this formation outcrops in the coastal section from Peralta to Porto Dinheiro. Several sauropod specimens from the Sobral Fm. were reported, highlighting the lectotype of *Lusotitan atalaiensis*. It was found in the Peralta cliffs, close to the Atalaia locality (Lourinhã). Lapparent and Zbyszewski (1957) firstly considered this specimen as a new species of *Brachiosaurus* (in that moment including two species, the North American *B. altithorax* and the African *B. brancai*). Posteriorly, Antunes and Mateus (2003) established the new genus, *Lusotitan*, to denominate this specimen. Mannion et al. (2013) proceeded to the systematic revision of the Peralta specimen, considering it as a basal macronarian, and a brachiosaurid with doubt. This specimen includes dorsal, sacral and caudal vertebrae, pelvic, forelimb and hindlimb elements (Fig. 4.14i-n; Lapparent and Zbyszewski, 1957; Antunes and Mateus, 2003; Mannion et al., 2013). In Peralta, several sauropod teeth were found, including heart- (Mocho et al., 2012, in press), spatulate- (Fig. 4.14a-b, Mocho et al., 2011), and compressed cone-chisel-shaped teeth (Fig. 4.14c-f). In addition, some isolated bones from this region were also found (Fig. 4.14g).

Porto das Barcas is another relevant locality concerning dinosaur occurrences. The holotype of the ornithopod *Eousdryosaurus* (Dantas et al., 2000; Escaso et al., 2014), and nests with theropods eggs tentatively related with the *Torvosaurus* genus (Castanhinha et al., 2009; Araújo et al., 2012, 2013), were found there. Several classic specimens from Porto das Barcas were referred to *Apatosaurus alenquerensis* by Lapparent and Zbyszewski (1957), including caudal vertebrae (MG 8800, 8805). MG 30390 is an unpublished partial skeleton that represents an indeterminate eusauropod, according the presence of procoelous anterior caudal vertebrae. Another partial skeleton from Porto das Barcas is housed in ML (ML 351), including a partial caudal series, sacrum and fibula (Antunes and Mateus, 2003; Mateus, 2005). Antunes and Mateus (2003) and Mateus (2005) related this specimen to *Lourinhasaurus alenquerensis*. Nevertheless, this specimen does not bear available features that support this taxonomic approach. The detailed preparation and study of this material is in process (comm. pers., RC). Other specimens from this locality are housed in ML and SHN (Mateus, 2005, pers. observ, PM), including heart-shaped teeth (Mocho et al., 2012, in press), and compressed cone-chisel shaped teeth (e.g. SHN 576). From Lage Fria (Porto das Barcas), Tschopp and Mateus (2012) described a sternal plate (ML 684) suggesting that might pertain to *Turiasaurus riodevensis* or *Lusotitan atalaiensis*. Lapparent and Zbyszewski (1957, pl. XIII, fig. 31-33) referred one vertebra from Porto das Barcas (MMLT 602528) to a posterior dorsal vertebra of *Megalosaurus pombali*. However, it corresponds to an anterior caudal vertebra of an indeterminate sauropod. Another sauropod caudal vertebra (MMLT 602529) from Porto das Barcas was found in the collections of the MMLT, and probably corresponds to a vertebra referred by Lapparent and Zbyszewski (1957, pg. 38). This vertebra probably represent an indeterminate sauropod.

The Tithonian Bombarral Formation outcrops in the coastal section from Praia de Areia Branca to Paimogo (including Vale de Frades) (Fig. 4.11a). This formation transits to the Sobral

Figure 4.14. Cranial and postcranial sauropod remains from sediments of the Sobral Fm. and Bombarral Fm. of the coastal sector of Praia da Consolação-Lourinhã-Torres Vedras: a-b) ?Turiasauria indet., spatulate-shaped tooth (SHN 122, Peralta) in labial (a) and lingual (b) views; c-d) Titanosauriformes indet., compressed cone-chisel-shaped teeth (SHN 550 and 551, Peralta) in labial (c, e) and lingual (d, f) views; (g) Sauropoda indet., left dorsal transverse process (MG 8809, Atalaia) in dorsal view; h) Eusauropoda indet., anterior caudal vertebra in posterior view (MNHN/UL.Din.027, Praia da Areia Branca); i-n) lectotype material of *Lusotitan atalaiensis* (Peralta), anterior caudal vertebra MG 4985-2 (j) and MG 4985-4 (i) in posterior view, left astragalus (MG 4803) in posterior view (k), right humerus (MG 4989) in anterior view (l), right radius (MG 4958) in anterior view (m), right tibia (MG 4981) in posterior view (n); o) Titanosauriformes indet., a proximal end of left femur (MG 4986, Praia da Areia Branca) in anterior view; p-s) Eusauropoda indet., partial tail (GeoFCUL(AB), Areia Branca), middle chevron in posterior chevron, in middle caudal vertebra GeoFCUL(AB) 22 in anterior view (q), GeoFCUL(AB) 21 lateral view (r), GeoFCUL(AB) 20 in posterior view (s). Black scale bar: 10 cm; Gray scale bar: 1 cm. See Anatomical abbreviations for abbreviations.

Fm. (on the Forte of Paimogo) and Praia de Amoreira-Porto Novo Fm. (Hill, 1988; Manuppella et al., 1999). Furthermore, the Bombarral Fm. outcrops in a wide area on the east of the Lourinhã Fault, from A-dos-Cunhados to Alcobaça (area included in the Bombarral-Alcobaça Sub-basin by Taylor et al., 2013). The Bombarral Fm. was deposited in a lacustrine to fluvial environment (Manuppella et al., 1999).

West of Lourinhã Fault, the Bombarral Formation. outcrops between Peralta and Vale de Frades (south of Paimogo), and south of Santa Rita up to Santa Cruz town. Some bones coming from the Bombarral Fm. were reported by Lapparent and Zbyszewski (1957). A partial left femur (Fig. 4.14o, MG 4986) was found in Praia da Areia Branca, and was firstly related to *Brachiosaurus atalaiensis* (Lapparent and Zbyszewski, 1957). It has been recently reattributed to an indeterminate titanosauriform (Mannion et al., 2013). Two caudal vertebrae housed in the paleontological collections of the MNHNC were recovered in Areia Branca: an anterior caudal vertebra previously referred to *Brachiosaurus atalaiensis* (Lapparent and Zbyszewski, 1957), and a procoelous anterior caudal centrum (Fig. 4.14g, MNHN/UL.Din.027) referred to *Apatosaurus alenquerensis* (Lapparent and Zbyszewski, 1957). The information on the first one is scarce and just can be considered as an indeterminate sauropod. The second one is recognized as belonging to an indeterminate eusauropod, based on the presence of procoelous caudal vertebra, feature present in turiasaurs (e.g. Casanovas et al., 2011). Lapparent and Zbyszewski (1957, pg. 17) referred the occurrence of a small femur of a sauropod from Vale de Frades, but its present whereabouts is unknown.

Yagüe et al. (2006) published a partial tail found in Praia de Areia Branca (GeoFCUL (AB), Lourinhã), recovered by members of the Department of Geology of Sciences Faculty of Lisbon University (GeoFCUL). This specimen comprises several middle caudal vertebrae and chevrons (Fig. 4.14p-s), and was tentatively attributed to a basal Macronaria (Yagüe et al., 2006). The comparison with more complete caudal series (e.g. Osborn and Mook, 1921; McIntosh et al., 1996a, b; Mannion et al., 2013), allow recognize that the most anterior preserved vertebra probably corresponds to the thirteenth or fourteenth caudal. The absence of caudal ribs up to the twentieth caudal vertebrae is common in eusauropods (Upchurch et al., 2004). Yagüe et al. (2006) used this feature to place this specimen within that clade. Nevertheless, the phylogenetic distribution of this feature in some basal sauropods is unknown and we prefer to attribute to a probable eusauropod. This specimen does not present features supporting its placement within Macronaria and the hypothesis proposed by Yagüe et al. (2006) is refuted. An unpublished procoelous anterior caudal vertebra (MMPM.P/73) of an indeterminate eusauropod was collected in Paimogo. No precise location was given for this element. Therefore, and taking into account that in this locality outcrops sediments of both the Bombarral and Sobral Formations (Hill, 1988; Mannuppella et al., 1999), its precise stratigraphic context is not known. South of Santa Rita outcrops an important section of the Bombarral Fm. and some unpublished elements were collected herein, including some presacral vertebrae preserved in the SHN (SHN 006, 535).

In conclusion, the Praia da Consolação-Lourinhã-Torres Vedras coastal sector presents the most diverse Portuguese Upper Jurassic fossil record concerning the sauropods, being composed by basal eusauropods such turiasaurs (e.g. *Zby atlanticus*), diplodocines (e.g. *Dinheirosaurus lourinhanensis* and SHN (JJS) 177), basal macronarians (e.g. SHN 181), and titanosauriforms including brachiosaurids (e.g. *Lusotitan atalaiensis*). The presence of camarasaurid macronarians cannot be confirmed in this area, but the systematic study of SHN 002 will allow testing the affinities of this specimen with *Lourinhasaurus alenquerensis*, as well as, with Camarasauridae.

4.5.2. Arruda Sub-Basin

The Arruda Sub-basin is relatively poor in dinosaur fossil-sites (Figs. 4.15, 4.16), fact that is probably related with the absence of a wide area of exposed Upper Jurassic outcrops. This half-graben basin has a similar Upper Jurassic stratigraphy than the Turcifal Sub-basin (Kullberg et al., 2006, 2010; Fig. 4.2). The stratigraphy of the Arruda Sub-basin was mainly defined by Leinfelder (1993). From this sub-basin, the vertebrate fossil record is mainly composed by sauropod dinosaurs (Lapparent and Zbyszewski, 1957; Antunes and Mateus, 2003; Ortega et al., 2009).

One of the most complete sauropod individuals in the European Upper Jurassic record was discovered by the North American geologist Harold Weston Robbins in the Arruda Sub-basin, during his employment by Portuguese Petroleum Company. This specimen was found north of a ruined windmill named Moinho do Carmo (Lapparent and Zbyszewski, 1957). Lapparent and Zbyszewski (1957) indicated that the fieldwork was carried out by the staff of the Serviços Geológicos de Portugal in June 1949, under the direction of the geologist Georges Zbyszewski. The sole

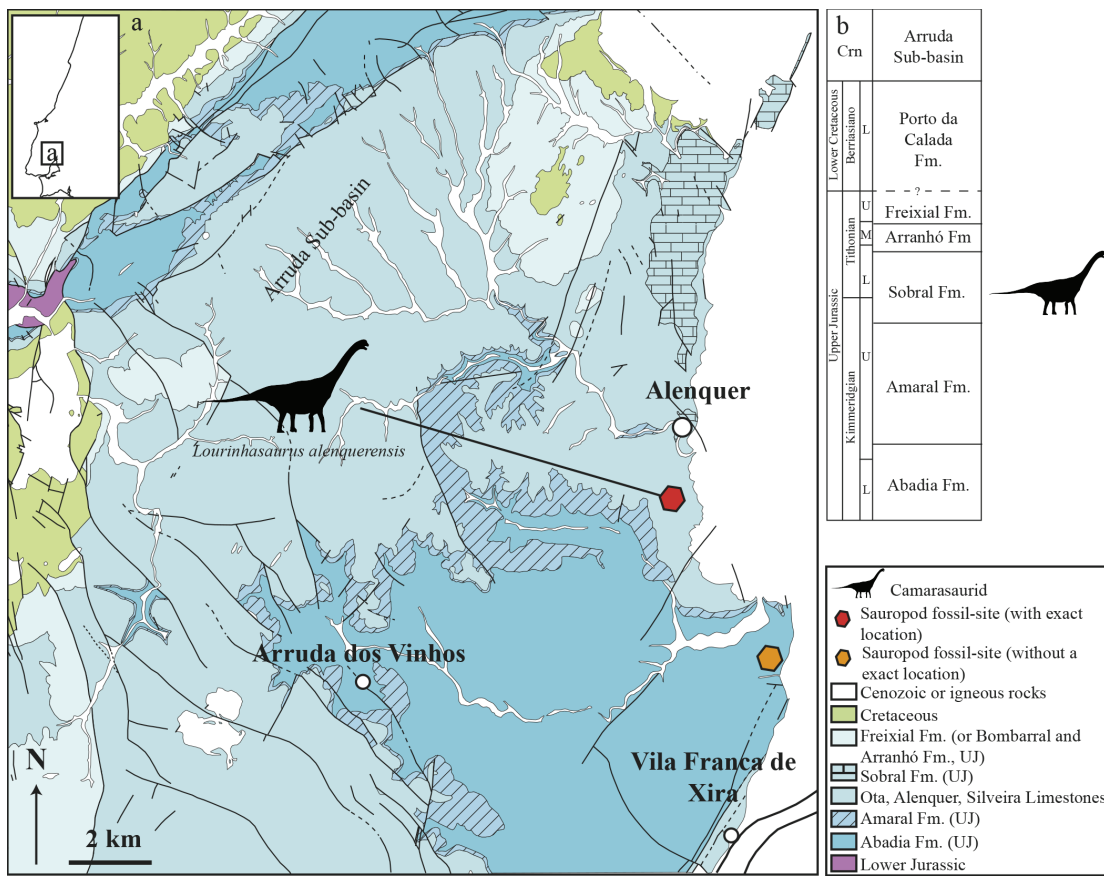
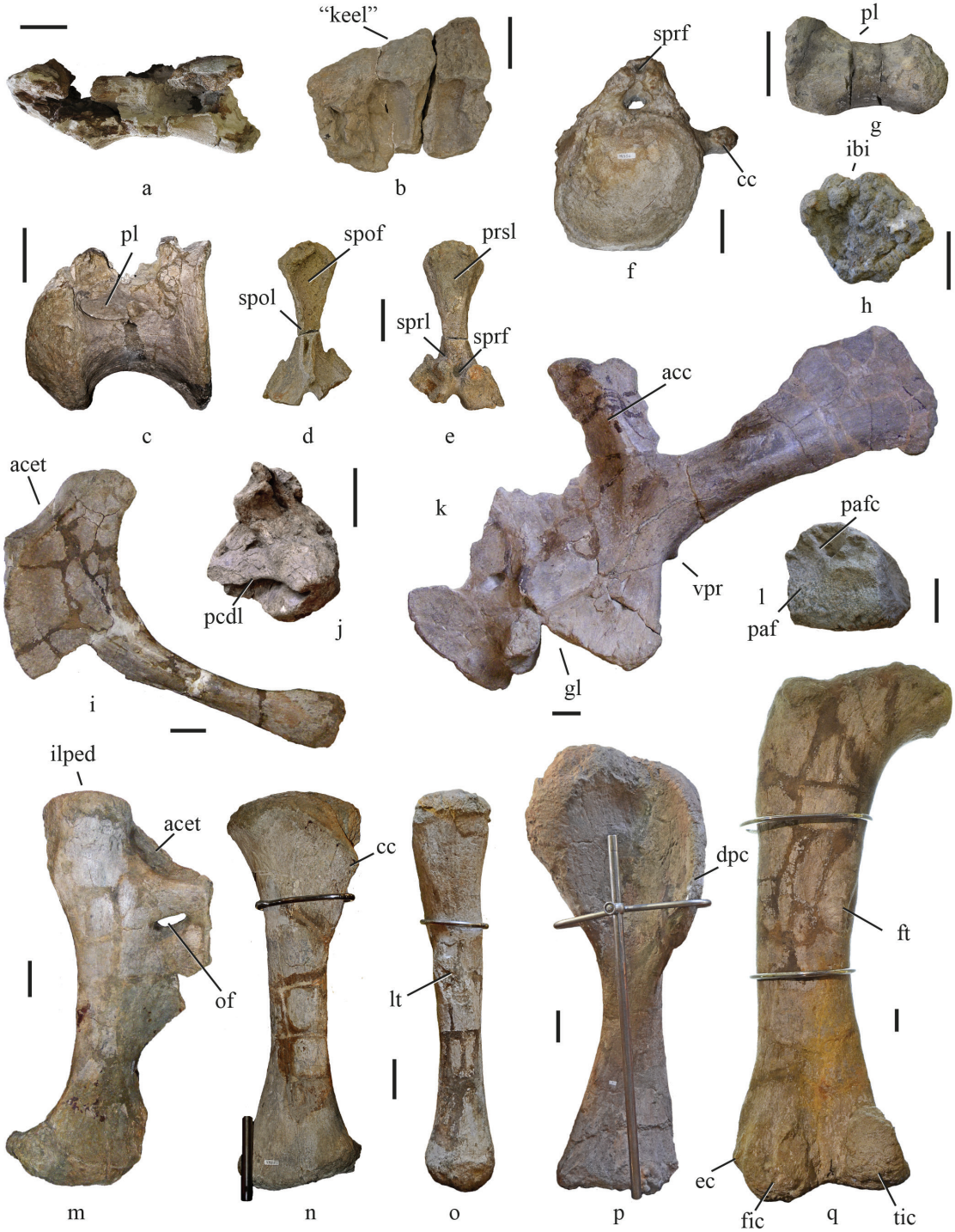


Figure 4.15. a) Geological map of Arruda Sub-basin (modified Zbyszewski and Torre de Assunção 1965; Zbyszewski et al., 1966) with the localities yielding fossil remains referred to Sauropoda. b) Simplified stratigraphy of the Kimmeridgian-Tithonian sequence for Arruda Sub-basin based on Kullberg et al. (2006) with the stratigraphic distribution of the main sauropod clades identified in this area. Crn – Chronostratigraphy.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specimen identified was used to define a new species of *Apatosaurus*: *Apatosaurus alenquerensis* (Lapparent and Zbyszewski, 1957). Dantas et al. (1998) established a new genus for this taxon, *Lourinhasaurus*, proposing the new combination *Lourinhasaurus alenquerensis*. The specimen is composed by cervical, dorsal, sacral and anterior caudal vertebrae, dorsal ribs, scapular and pelvic elements, and bones of the hindlimb and forelimb (Fig. 4.16a-f, h-q; Lapparent and Zbyszewski, 1957; Mocho et al., 2014a). The recent systematic revision of the *Lourinhasaurus* lectotype confirmed the placement of this taxon in Camarasauridae clade (Mocho et al., 2014a), a hypothesis previously suggested by other authors (McIntosh, 1990a, b; Wilson and Sereno, 1998).

A partial opisthocoelous dorsal centrum (Fig. 4.16g, MG 4799) was found in Castanheira (Vila Franca de Xira), in sediments of the Abadia Formation (Leinfelder and Wilson, 1989). This element was firstly described as a metatarsal V by Lapparent and Zbyszewski (1957), but Mannion et al. (2013) reinterpreted it as a procoelous caudal vertebra. There is some unpublished fossils deposited in the MG that might come from Alenquer or inclusively from Moinho do Carmo, but these specimens present a distinct state of preservation and different taxonomic features when compared with the material referred to *Lourinhasaurus* lectotype. This allow us to raise a reasonable doubt related with their locality of origin.

The scarce record of the Arruda Sub-basin only allow us to identify an indeterminate neosauropd and a camarasaurid macronarian (*Lourinhasaurus alenquerensis*) preserved in sediments of the Abadia Formation and the Sobral Formation, respectively (Fig. 4.15a-b).

4.5.3. Turcifal Sub-basin

The Turcifal Sub-basin is a half-graben basin, located west of the Arruda Sub-basin. The stratigraphy of both sub-basins is similar (Kullberg et al., 2006, 2010). Several authors provided recent updates on the stratigraphy of this area (e.g. Pereda-Suberbiola et al., 2005; Kullberg et al., 2006, 2010). Their Upper Jurassic outcrops are not so extensive than those of the Bombarral Sub-basin. Nevertheless, dinosaur fossil-sites are particular abundant, being mainly concentrated on the coastal sector (Figs. 4.17, 4.18). A diverse dinosaur fauna, composed by sauropods, theropods, thyreophorans and ornithopods, has been identified. This sub-basin is bounded on the north by the Torres Vedras-Montejunto Fault and on the east by the Runa Fault, which separates it from the Arruda Sub-basin (e.g. Wilson, 1988; Fig. 4.2).

Theropods are represented by allosaurids, with an important fossil site coming from Cambelas (Moniz et al., 2002; Malafaia et al., 2009b; Ortega et al., 2009). Thyreophoran dinosaurs

Figure 4.16. Postcranial sauropod remains from the Arruda Sub-basin: a-f, h-q) lectotype material of *Lourinhasaurus alenquerensis* (Moinho do Carmo), middle-to-posterior cervical centrum (MG 30373) in lateral view (a), fused sacral neural spines (MG 30376) in left view (b), dorsal centrum (MG 4956) in left view (c), anterior caudal neural spine (MG 30374) in posterior (d) and anterior (e) views, anterior caudal centrum (MG 4956) anterior view (f), middle dorsal neural spine (MG 30384) in posterior view (h), left ischium (MG 4957) in lateral view (i), posterior cervical neural spine (MG 30379) in right view (j), left scapula and coracoids (MG 5780) in lateral view (k), left astragalus (MG 30375) in proximal view (l), left pubis (MG 4970) in lateral view (m), left tibia (MG 4983) in anterior view (n), left fibula (MG 4984) in lateral view (o), left humerus (MG 2) in anterior view (p) and left femur (MG 4931) in posterior view (q); g) Neosauropoda indet., partial dorsal centrum (MG 4799, Castanheira) in right view. Black scale bar: 10 cm. See Anatomical abbreviations for abbreviations.

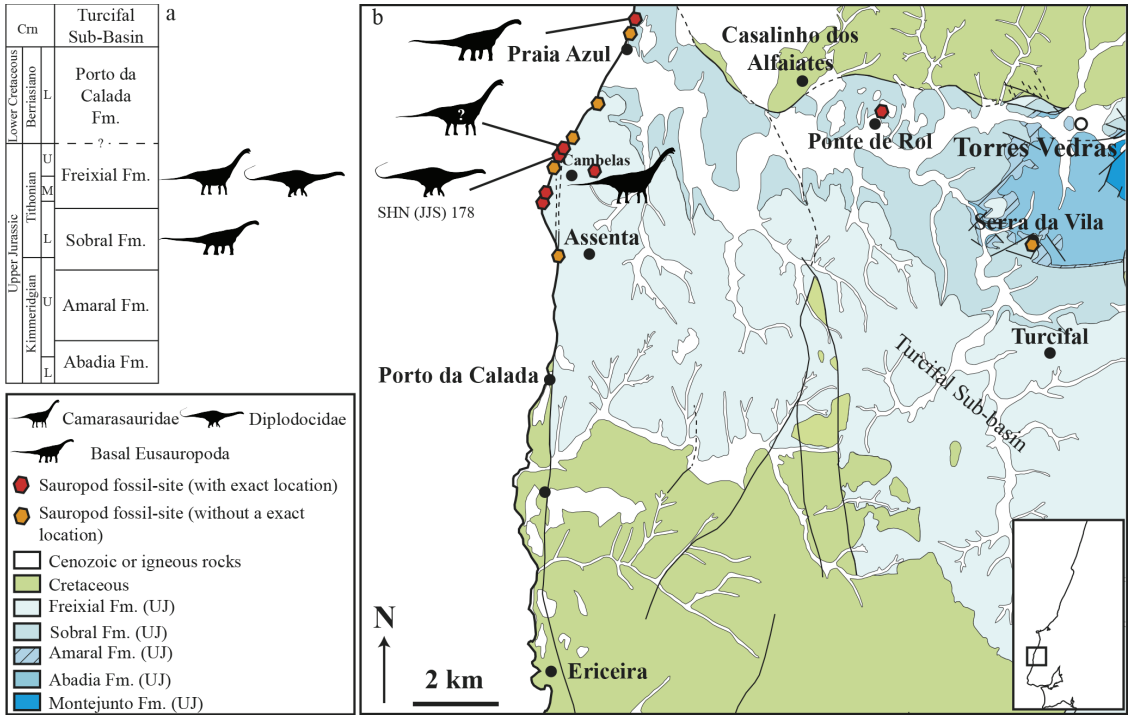

Figure 4.17. a) Simplified stratigraphy of the Kimmeridgian-Tithonian sequence for Turcifal Sub-basin based on Pereda-Suberbiola et al. (2005), Kullberg et al. (2006) and Schneider et al. (2009) with the stratigraphic distribution of the main sauropod clades identified in this area. b) Geological map of Turcifal Sub-basin (modified from Zbyszewski et al., 1955) with the localities yielding fossil remains referred to Sauropoda. Crn – Chronostratigraphy.

are represented in this sub-basin by the holotype of the ankylosaur *Dracopelta zbyszewski* (Galton, 1980; Pereda-Suberbiola et al., 2005), found in the sediments of the Freixial Formation in Assenta (Torres Vedras). Another partial ankylosaur skeleton was found in the Porto Calada locality (Mafra), and preliminary considered as 'polacanthid' nodosaurid (Mateus et al., 2013). Material related to the stegosaur *Dacentrurus* was also described in the Moçafaneira locality (Escaso et al., 2007b).

Furthermore, non-dinosaur vertebrates are also present in the sediments of this basin. Among them, the turtle record is very relevant, including the type material of "*Plesiochelys*" *choffati* and *Hylaeochelys kappa* (Sauvage, 1897-98; Pérez-García et al., 2008; Pérez-García and Ortega, 2013, Pérez-García, 2015). The record of crocodiles is also abundant, not only represented by bones, but also by a nest with eggs, found in the Cambelas area (Russo et al. 2014, 2015).

The sauropods are well-represented in the Turcifal Sub-basin. Most of the record of this clade correspond to recent findings. Therefore, relatively scarce information is so far available due to most of these specimens are now under study and/or in preparation. A short section of the Praia de Amoreira-Porto Novo Formation (fluvial environment) is placed south of Santa Cruz locality. A middle caudal vertebra (Fig. 4.18j, MG 4802) was collected in this area and was attributed to *Apatosaurus alenquerensis* (Lapparent and Zbyszewski, 1957). This vertebra is considered herein as belonging to an indeterminate sauropod due to no diagnostic features are present in order to proceed to a more detail taxonomic approach.

Most of the sauropod discoveries in the Turcifal Sub-basin come from the Sobral (marine to deltaic environment) and Freixial (delta plain to fluvial environment) Formations (Hill, 1988;

Manuppella et al., 1999). The Sobral Fm. outcrops on the northern sector of this sub-basin. MG 8803 is an unpublished element coming from Serra da Vila (locality referred by Lapparent and Zbyszewski, 1957, fig. 1) identified herein as distal end fragment of a tibia (Fig. 4.18k-l). In Ponte de Rol (Torres Vedras) highlights an unpublished set of sauropod remains (Fig. 4.18o-p), which includes dorsal and caudal vertebrae, and several appendicular elements (scapula, femur, radius, etc.), probably belonging to a single individual (SHN 532). A detailed study about this specimen is in progress in order to provide a more detailed systematic approach.

Praia Azul (Torres Vedras) is a locality with several referred fossil-sites. Herein, some sauropod specimens have been collected, including a set composed by dorsal and sacral vertebrae and dorsal ribs of a single individual (SHN 533), with an appreciable size (e.g. high neural spines, transverse processes dorsolaterally projected), extracted in 2014 by the SHN. From this locality, other vertebrate groups are also reported (e.g. Pérez-García, 2015). Several unpublished sauropod specimens are deposited in the paleontological collections of the SHN, including a compressed cone-chisel-shaped tooth (SHN 549), as well as some unprepared partial skeletons and isolated bones. Some caudal vertebrae (MG 8804, MG 25254.2-4) were found close to Maceira (Torres Vedras). In particular, MG 8804 (Fig. 4.18n) was considered as *Lusotitan atalaiensis* by Lapparent and Zbyszewski (1957) and Mateus (2005).

Three of the most important quarries with sauropod dinosaurs of the Turcifal Sub-basin are located near Cambelas locality, where the Freixial Formation outcrops. One of them is located in Casal da Costa, where sauropod appendicular and axial material (Fig. 4.19, SHN 531), including dorsal vertebrae, as well as material of other groups of dinosaurs (theropods and ornithischians), turtles and crocodilyforms were recovered. The dorsal vertebrae from Casal da Costa share a morphology similar to those of *Camarasaurus supremus* (Mocho et al., 2013b). Some of these specimens were recently recovered from the field, and are now under preparation. Several occurrences were also reported on the Cambelas cliffs, including a site where several elements, probably from the same individual, were collected. This sauropod (SHN (JJS) 178) is composed by axial and appendicular elements (Fig. 4.18q-s), including pelvic girdle and hindlimb remains (Mocho et al., 2014b). It was preliminary related with Diplodocidae by the presence of a markedly expansion of the ischiatic distal end (Mocho et al., 2014b). The pronounced lateral bulge on the femur observed in this specimen, generally considered as a synapomorphy of Titanosauriformes (e.g. Wilson, 2002), also occurs in *Diplodocus* (e.g. Hatcher, 1901). A preliminary evaluation of SHN (JJS) 178 suggests a close relationship to an unpublished diplodocid recovered in Valmitão (SHN (JJS) 177), which shares affinities with the Diplodocinae clade (Mocho et al., 2014b). Finally, a partial skeleton with axial and appendicular elements (Fig. 4.18g-h, SHN 529) were also found in a distinct fossil-site from the Cambelas locality, and bears an anterior caudal neural spine with a delta-shaped distal end, common in camarasaurids (Ikejiri, 2005; Mocho et al., 2014a). Several sauropod occurrences are identified in the Freixial Fm. section of Cambelas, Gentias and Assenta cliffs, including several teeth, axial and appendicular elements (Fig. 4.18i, m). The collected teeth include heart- (Fig. 4.18a-b; see also Mocho et al., 2012, in press); spatulate-shaped teeth (Fig. 4.18e, see also Mocho et al., 2011) and a compressed cone-chisel-shaped tooth (Fig. 4.18c-d). In Porto Barril (Mafra), a possible unpublished middle cervical vertebra (Fig. 4.18f, SHN 528) was found, bearing a well-developed camellate tissue bone similar to the tissue present by basal titanosauriforms and mamenchisaurids (following Wedel, 2003).

In conclusion, the Turcifal Sub-basin represents a relatively continuous Upper Jurassic sequence, with a rich sauropod record. The sauropod faunas identified in the Turcifal Sub-basin are composed by basal eusauropods (probably turiasaurs), diplodocids (with probably diplodocine affinities that needs to be confirmed), basal macronarians including camarasaurids and titanosauriforms.


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Figure 4.19. Dorsal vertebrae in the field of a partial skeleton (SHN 531) collected in Casal da Costa (Cambelas) and might a member of Camarasauridae clade.

Figure 4.18. Cranial and postcranial sauropod remains from the Turcifal Sub-basin: a-b) ?Turiasauria, heart-shaped tooth (SHN (JJS) 140, Cambelas) in labial (a) and lingual (b) views; c-d) Titanosauriformes indet., compressed cone-chisel-shaped tooth (SHN 580, Assenta) in lingual (c) and labial (d) views; e) Eusauropoda indet., spatulate-shaped tooth (SHN 519, South of Foz do Sizandro) in lingual view; f) Eusauropoda indet., middle cervical vertebra (SHN 528, Porto Barril) with camellae tissue bone (sensu Wedel, 2003); g-h) ?Camarasauridae indet., anterior caudal neural spine (SHN 529, Cambelas) in left (g) and anterior (h) views; i) Sauropoda indet., right tibia (SHN 527, Cambelas) in proximal view; j) Sauropoda indet., middle caudal vertebra (MG 4802, Santa Cruz) in right view; k-l) partial distal end of a ?left tibia (MG 8803, Serra da Vila) in anterior (k) and distal (l) views; m) humerus distal end (SHN 584, Assenta) in anterior view; n) cf. *Lusotitan atalaiensis*, middle caudal vertebra (MG 8804, Maceira) in right view; Sauropoda indet., partial skeleton (SHN, 532, Ponte de Rol), posterior caudal vertebra in left view (o) and distal end of a right femur in anterior (p) views; Diplodocidae indet., partial skeleton (SHN (JJS) 178, Cambelas), sacral neural spines in anterior (q) and left (r) views and right femur in anterior (s) view.). Black scale bar: 10 cm; Gray scale bar: 1 cm. See Anatomical abbreviations for abbreviations.

4.6. SAUROPOD PALEOBIODIVERSITY AND STRATIGRAPHIC DISTRIBUTION FOR THE LUSITANIAN BASIN

The Upper Jurassic record of the Lusitanian Basin is rich in dinosaur occurrences and, in particular, in fossil-sites with sauropod remains. The Portuguese Upper Jurassic sauropods have been the focus of several recent papers, including new material (Yaguë et al., 2006; Mocho et al., 2011, 2012, 2013a, b, 2014b, 2015, in press; Mannion et al., 2012; Mateus et al., 2014), as well as the systematic revision of previously established sauropod taxa (Mannion et al., 2012, 2013; Mocho et al., 2014a). A stratigraphic context for the sauropod record reported in the Lusitanian Basin is proposed here for the first time. In addition, we also report several new occurrences that evidence the potential of the Portuguese record for understanding the paleobiodiversity and evolutionary history of the Iberian Upper Jurassic sauropod faunas. The stratigraphic distribution suggests that the major clades (i.e. Eusauropoda, Macronaria, Diplodocoidae and Titanosaurifromes) are present along the continental deposits of sedimentary sequence dated from the lower Kimmeridgian to the upper Tithonian. The only exceptions are Camarasauridae, being only identified in the Sobral and Freixial Formations, and Diplodocinae, absent in the Sobral Fm. In the former group, this situation might be explained by the presence of a small sample of specimens confidently assigned to Camarasauridae.

Turiasauria is a eusauropod clade, firstly identified on the Upper Jurassic of the Lusitanian Basin by Royo-Torres et al. (2006). Its heart-shaped tooth morphology has been proposed as exclusive of turiasaurs (Royo-Torres et al., 2006, 2009; Mocho et al., 2012; Royo-Torres and Upchurch, 2012). The wide stratigraphic (Middle Jurassic to Lower Cretaceous) and paleogeographic (Europe and Africa) range for this shape suggest that this morphology of teeth could be a feature of a more inclusive group or a convergent feature in other sauropod groups (Mocho et al., in press). The heart-shaped teeth present a wide stratigraphic distribution along the Upper Jurassic levels of the Lusitanian Basin, being present in Alcobaça, Praia de Amoreira-Porto Novo, Sobral, Bombarral and Freixial Formations.

In spite of the absence of a phylogenetic context based on a cladistics analyses, *Zby atlanticus*, found in Praia de Amoreira-Porto Novo Formation, is the only specimen confidently assigned to Turiasauria (Mateus, 2005; Mateus et al., 2014). Nevertheless, other specimens found in the Portuguese Upper Jurassic have been preliminary considered as non-neosauropod eusauropods, and they could represent turiasaurian forms (non-turiasaurian eusauropods have not been so far identified for the Iberian Upper Jurassic record). The basal eusauropods present a wide stratigraphic range in the Upper Jurassic levels of Portugal (Fig. 4.20). Basal eusauropod remains have been recovered in the fluvial Praia de Amoreira-Porto Novo Fm. (e.g. ML 368; SHN 530), the marine to deltaic Sobral Fm. (e.g. SHN 533), and the fluvial to deltaic Bombarral Fm (Fig. 4.14h).

Diplodocoidea is a clade recorded from the upper Kimmeridgian up to the probably upper Tithonian of the Portuguese Upper Jurassic record (Fig. 4.20). This clade is represented by one described diplodocine *Dinheirosaurus lourinhanensis*, and material considered as belonging to an indeterminate diplodocines (Mannion et al., 2012; Mocho et al., 2014b, 2015; Tschopp et al., 2015). Based on the material from Moita dos Ferreiros (ML 418), Mannion et al. (2012) suggested the presence of, at least, two diplodocid forms in the Portuguese Upper Jurassic levels. However, the specimen from Moita dos Ferreiros was posteriorly considered as an indeterminate diplodocine by Tschopp et al. (2015). Diplodocines have been recorded on the Praia de Amoreira-Porto Novo, Bombarral and Freixial Formations. The presence of this clade in Alcobaça (marine up to fluviolacustrine environments) or Sobral (deltaic environment) Formations is so far unreported.

Basal macronarians are a diverse group in the Iberian territory, being represented by the Portuguese *Lourinhasaurus* and *Lusotitan*, and the Spanish *Aragosaurus* and *Galveosaurus* (e.g.

Barco, 2009; Mannion et al., 2013; Mocho et al., 2013a, b, c, 2014a; Royo-Torres et al., 2014a), and a putative Portuguese new form (SHN 181). *Galveosaurus* was recovered as a turiasaur by Royo-Torres et al. (2006, 2009, 2012), Royo-Torres and Upchurch (2012) and Mocho et al. (2014a). Several indeterminate specimens assigned to this clade have been found in the Upper Jurassic record of the Lusitanian Basin, being present in the Alcobaça, Praia de Amoreira-Porto Novo, Sobral, Freixial and Bombarral Formations. Therefore, a stratigraphic range from the lower Kimmeridgian to the probably upper Tithonian is recognized (Fig. 4.20). Camarasauridae was clearly identified on the Sobral Fm. (*Lourinhasaurus alenquerensis*) and in the Freixial Fm. (SHN 531). Nevertheless, the systematic context of several other specimens needs to be evaluated (e.g. SHN 002, from the Praia de Porto-Novo Fm., found in Porto Novo, Torres Vedras; and SHN 529, from the Freixial Fm., found in Cambelas, Torres Vedras), in order to understand the true stratigraphic range of this group. At the moment, Camarasauridae is recorded from the upper Kimmeridgian-basal Tithonian to the probably upper Tithonian (Fig. 4.20). If the Porto Novo specimens correspond to a Camarasauridae member, the stratigraphic range of the clade will be upper Kimmeridgian-probably upper Tithonian.

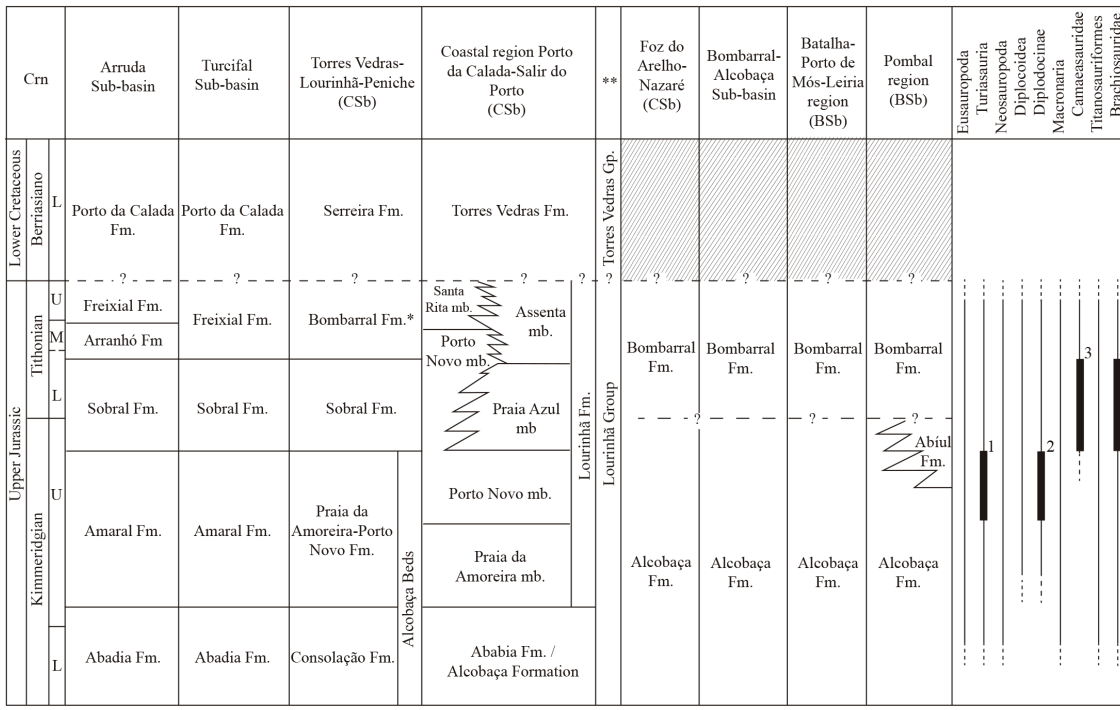

Figure 4.20. Stratigraphic correlation between the nomenclature proposed for *i*) Turcifal Sub-basin (based on Pereda-Suberbiola et al. 2005, Kullberg et al. 2006, Schneider et al. 2009), *ii*) Arruda Sub-basin (Kullberg et al., 2006); *iii*) Consolação Sub-basin areas: Torres Vedras-Lourinhã-Peniche (based on Manuppella et al. 1999), Foz do Arelho-Nazaré coastal sector (Kullberg et al., 2006; Azerêdo et al., 2010); *iv*) Bombarral-Alcobaça Sub-basin (based on Azerêdo et al., 2010); *v*) Batalha-Leiria region (based on Manuppella et al., 2000; Kullberg et al. 2006; Escaso et al., 2007) and *vi*) Pombal region (Kullberg et al., 2006; Malafaia et al., 2010). The stratigraphy proposed by Hill (1988) for the coastal sector from Porto da Calada to Salir do Porto is also plotted. Crn – Chronostratigraphy; ***sensu* Yagüe et al., 2006. The right column shows the known stratigraphic distribution of the main sauropod clades along the Kimmeridgian-Tithonian sedimentary sequence in the Lusitanian Basin. The black bar indicates the known distribution of the established sauropod taxa (1, *Zby atlanticus*; 2, *Dinheirosaurus lourinhanensis*; 3, *Lourinhasaurus alenquerensis*; 4, *Lusotitan atalaiensis*). BSb, Bombarral Sub-basin (following Kullberg et al., 2006); CSb, Consolação Sub-Basin (following Taylor et al., 2013).

The Titanosauriformes clade is recorded in the Alcobaça, Praia de Amoreira-Porto Novo, Sobral, Bombarral and Freixial Formations. *Lusotitan atalaiensis* is a putative brachiosaurid (Mannion et al., 2013) coming from the Sobral Fm. Besides the presence of several specimens with titanosauriform affinities, *Lusotitan* might represents the strongest evidence for the presence of this clade during the Upper Jurassic of the Lusitanian Basin. If the presence of maxillary teeth twisted axially through an arc of 30–45° correspond to a brachiosaurid synapomorphy (as suggested by D'Emic, 2012), several teeth found on the Lusitanian Basin might be attributed to Brachiosauridae, increasing the stratigraphic range of this clade. New discoveries will improve our knowledge about the Iberian titanosauriforms, mainly based by on incomplete specimens.

Several new sauropods specimens, belonging to several clades, are reported herein. Nevertheless, the collections of ML and SHN still housed many specimens that need to be prepared, catalogued and studied (see Mateus, 2005; Mocho et al., 2013b, c, 2014b; pers. observ. PM). In addition, new relevant specimens have been recently discovered and extracted by MNHNC, SHN and ML. Herein, some of the most important sauropod occurrences were referred, including informative partial skeletons such as the specimen from Praia Vermelha (SHN (JJS) 179, Peniche); Porto das Barcas (ML 351, Lourinhã; see Antunes and Mateus, 2003; Mateus, 2005); Porto Novo (SHN 002, Torres Vedras); Praia da Corva (SHN 530, Torres Vedras); Santa Rita (SHN 534, Torres Vedras), Praia Azul (SHN 533, Torres Vedras) and Cambelas (SHN 529, Torres Vedras). The systematic study of all these occurrences will significantly improve the knowledge about the Portuguese Upper Jurassic sauropod faunas. The study of other so far unpublished specimens will also be informative, such as those including axial and appendicular elements, in particular the basal macronarians recovered in Casal da Costa (SHN 531, Torres Vedras) and Valmitão (SHN 181, Lourinhã); and the diplodocids from Valmitão (SHN (JJS) 177, related to Diplodocinae clade), and Cambelas (SHN (JJS) 178, Torres Vedras). They will allow us to understand the paleobiodiversity of Diplodocinae and Camarasauridae in the Upper Jurassic record of the Lusitanian Basin. SHN 181, from Valmitão (Praia de Amoreira-Porto Novo Formation, upper Kimmeridgian-basal Tithonian) is a specimen under description, and might represent a new basal macronarian, increasing the paleobiodiversity of the Portuguese Upper Jurassic sauropod faunas that will be composed by at least six putative taxa: one turiasaur (*Zby*), two different diplodocines (*Dinheirosaurus* and one indeterminate diplodocine); and at least three macronarians: one camarasaurid (*Lourinhasaurus*), one brachiosaurid (*Lusotitan*) and one non-camarasaurid basal macronarian (SHN 181).

4.7. CONCLUSIONS

The Upper Jurassic sauropod fossil record is well represent on the Upper Jurassic sequence of the Central Sector of the Lusitanian Basin, being particular abundant in the Bombarral and Turcifal Sub-basins. A stratigraphic context for the sauropod record reported in the Lusitanian Basin is proposed and several new specimens were reported herein for the first time. Sauropods are present along the continental deposits of the Lusitanian Basin, being recorded in the Alcobaça, Praia de Amoreira-Porto Novo, Sobral, Freixial, Bombarral Formations. Some areas of the Bombarral Sub-basin and Arruda Sub-basin still remain poorly understood due to the presence of scarce and incomplete material. The identified sauropod faunas are mainly composed by eusauropods (turiasaurs), diplodocids (diplodocines), basal macronarians (non-camarasaurids and camarasaurids) and titanosauriforms (some specimens with brachiosaurid affinities). No particular stratigraphic pattern was identified along the Upper Jurassic sequence, and the major clades are present along all the lower Kimmeridgian to the upper Tithonian levels.

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CHAPTER 5

Systematic review of the collections of Upper Jurassic sauropods at the Museu Geológico (Lisboa, Portugal)

Systematic review of the collections of Upper Jurassic sauropods at the Museu Geológico (Lisboa, Portugal)

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5.1. INTRODUCTION

The Upper Jurassic sediments of the Lusitanian Basin (Portugal) are known by the abundant occurrences of fossil vertebrates, in particular, dinosaurs, turtles and crocodyliforms (e.g. Sauvage, 1897-98; Lapparent and Zbyszewski, 1957; Dantas et al., 1992; Antunes and Mateus, 2003; Mateus, 2006; Ortega et al., 2006, 2009, 2013). The sauropod fossil record is particularly rich in this basin with several classical references (e.g. Sauvage, 1897-98; Lapparent and Zbyszewski, 1957), being represented by four taxa: the camarasaurid *Lourinhasaurus alenquerensis* (Lapparent and Zbyszewski, 1957; Dantas et al., 1998; Mocho et al., 2014a); the diplodocid *Dinheirosaurus lourinhanensis* (Dantas et al., 1992; Bonaparte and Mateus, 1999; Mannion et al., 2012), the basal macronaria *Lusotitan atalaiensis*, a putative brachiosaurid with doubt (Lapparent and Zbyszewski, 1957; Antunes and Mateus, 2003; Mannion et al., 2013) and the turiasaur *Zby atlanticus* (Mateus et al., 2014).

Despite some recent systematic revisions of the Portuguese Upper Jurassic taxa (*Dinheirosaurus* and *Lusotitan*, Mannion et al., 2012, 2013; and *Lourinhasaurus*, Mocho et al., 2013a, 2014a), several new occurrences (Royo-Torres et al., 2006, 2009; Yagüe et al., 2006; Mateus, 2009; Ortega et al., 2010; Mannion et al., 2012, Mocho et al., 2012, 2013a, 2014b; Mateus et al., 2014b) have been recently referred, denoting a more diverse scenario for sauropod faunas of the Lusitanian Basin during the Upper Jurassic. The presence of turiasaurs in the Portuguese Upper Jurassic has been suggested by the presence of isolate teeth and postcranial material (Mateus, 2009; Royo-Torres et al., 2009; Ortega et al., 2010; Mocho et al., 2012, in press). Mateus et al. (2014) defined a new turiasaur genus and species, *Zby atlanticus*, collected from Vale de Pombas. This specimen was firstly related to *Camarasaurus* (Mateus, 2005) and posteriorly to *Turiasaurus riodevensis* (Mateus, 2009).

The main part of the sauropod classical material collected by the Serviços Geológicos de Portugal on the Lusitanian Basin was deposited in the Museu Geológico (Lisboa, Portugal). These collections were referred since the end of the 19th century by Sauvage (1897-98) and during first half of the 20th century by Zbyszewski (1946) and Lapparent and Zbyszewski (1957). In the last years, some specimens were reviewed by several authors (Dantas et al., 1998; Antunes and Mateus, 2003; Mannion et al., 2013; Mocho et al., 2014a).

Herein, we propose a new systematic revision for the Upper Jurassic sauropod specimens collected along the Lusitanian Basin (Fig. 5.1) and deposited in the Museu Geológico (see Supplementary S.2), excluding two of the most complete specimens, the lectotypes of *Lourinhasaurus alenquerensis* and *Lusotitan atalaiensis*, recently reviewed by Mannion et al. (2013) and Mocho et al. (2013a, 2014a), respectively. For several years, some fragmentary specimens was been related with *Apatosaurus alenquerensis* or *Brachiosaurus atalaiensis*, now *Lourinhasaurus alenquerensis* and *Lusotitan atalaiensis*, respectively (Lapparent and Zbyszewski, 1957; Antunes and Mateus, 2003; Mateus, 2005). Most of them do not share any of the autapomorphies of these two Portuguese Upper Jurassic taxa.

The described material was mainly collected north of Lisboa in the Upper Jurassic sediments of the Turcifal, Arruda and Bombarral Sub-basins (Fig. 5.1a). On these sub-basins there are extensive areas where outcrops an Upper Jurassic to Lower Cretaceous sedimentary sequence. The Upper Jurassic beds are dated from middle Oxfordian to the base of Cretaceous (Fig. 5.1b) (Schneider et al., 2009), and represents a third rifting episode (Rasmussen et al. 1998, Kullberg et al. 2006). This episode of rifting is marked by an internal differentiation of the Lusitanian Basin resulting in the formation of several sub-basins (Turcifal, Arruda and Bombarral Sub-basins) followed by an important siliciclastic input which progressively filled these sub-basins (Hill, 1988; Pena dos Reis et al., 2000; Kullberg et al., 2006). Since the Kimmeridgian, the sedimentary sequence is marked by a strong siliciclastic nature, with

a continental signature in the top of the sequence up the top of the Upper Jurassic (e.g. Hill, 1988; Manuppella et al., 1999; Kullberg et al., 2006). Several formations are known by is richness in vertebrate fossil remains such as Alcobaça, Praia de Amoreira-Porto Novo (Fig. 5.1c), Sobral (Fig. 5.1d), Freixial and Bombarral Formations (Fig. 5.1b). In the Figure 5.2 there is a stratigraphic correlation between the nomenclature proposed for Arruda, Turcifal and Bombarral (including Alcobaça, Pombal, Batalha and Leiria regions) Sub-basins (based on Hill, 1988; Manuppella et al., 1999, 2000; Pereda-Suberbiola et al., 2005; Kullberg et al., 2006; Schneider et al., 2009; Azerêdo et al., 2010).

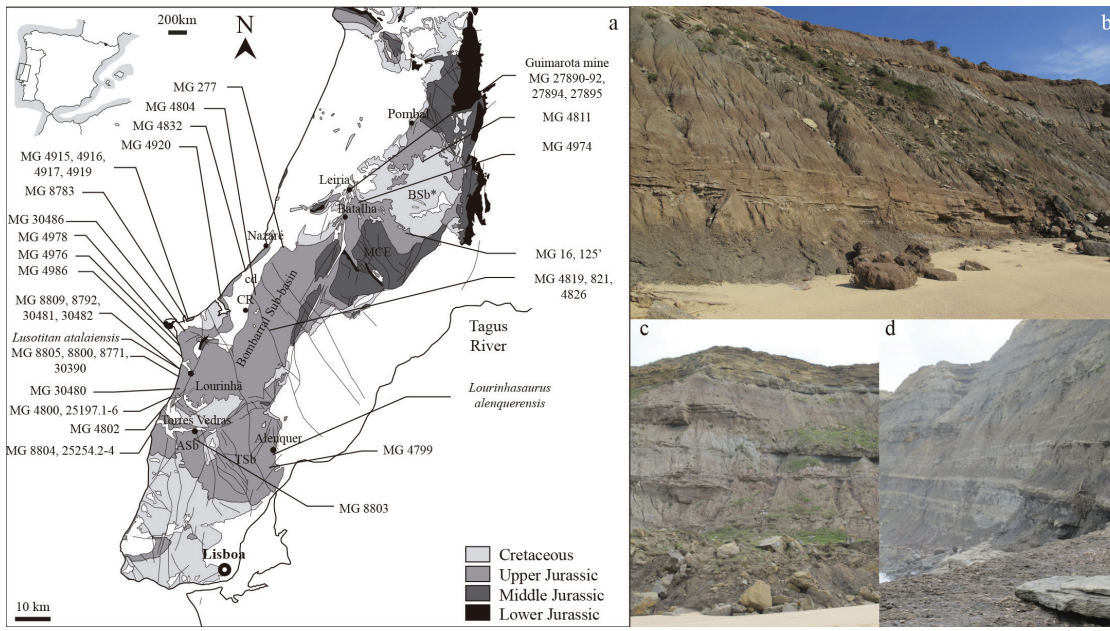


Figure 5.1. a) Geological map (adapted from Oliveira et al., 1992) showing the Portuguese Mesozoic levels and the localities of the material of Museu Geológico referred to sauropods and collected Lusitanian Basin. b) Fluvial to lacustrine deposits of the Bombarral Fm. outcropping in Paimogo (Lourinhã); c) Fluvial meandriforme deposits of Praia da Corva (Torres Vedras). d) Delta plain deposits of the Sobral Fm. in Praia Azul (Torres Vedras). ‘the locality is not precise; ASb- Arruda Sub-basin; BSb – Bombarral Sub-basin, cd – Caldas Diapir; CR – Caldas da Rainha town; TSb – Turcifal Sub-basin.

5.2. ANATOMICAL ABBREVIATIONS

acet, acetabulum; acpl, Anterior centroparapophyseal lamina; ant. spdl, anterior spinodiapophyseal lamina, at, anterior trochanter; bi, birfucation; cprf, centroprezygapophyseal fossa; cr, caudal rib; cprl, centroprezygapophyseal lamina; dpc, deltopectoral crest; lb, lateral bulge; lt, lateral trochanter; ltf, lateral trochanter fossa; pa, parapophyses; pca, posterior chevron articulation; pl, pleurocoel; pcdl, posterior centrodiapophyseal lamina; podl, postzygodiapophyseal lamina; post. spdl, posterior spinodiapophyseal lamina; prdl, prezygodiapophyseal lamina; pre, prezygapophyses; prpl, prezygoparapophyseal lamina; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; sut, suture line; tia, tibial articulation; tap, transverse aliform process; vh, ventral hollow; vlc, ventrolateral crest. The terminology applied for vertebrae laminae and fossae follows Wilson (1999, 2012) and Wilson et al. (2011), respectively.

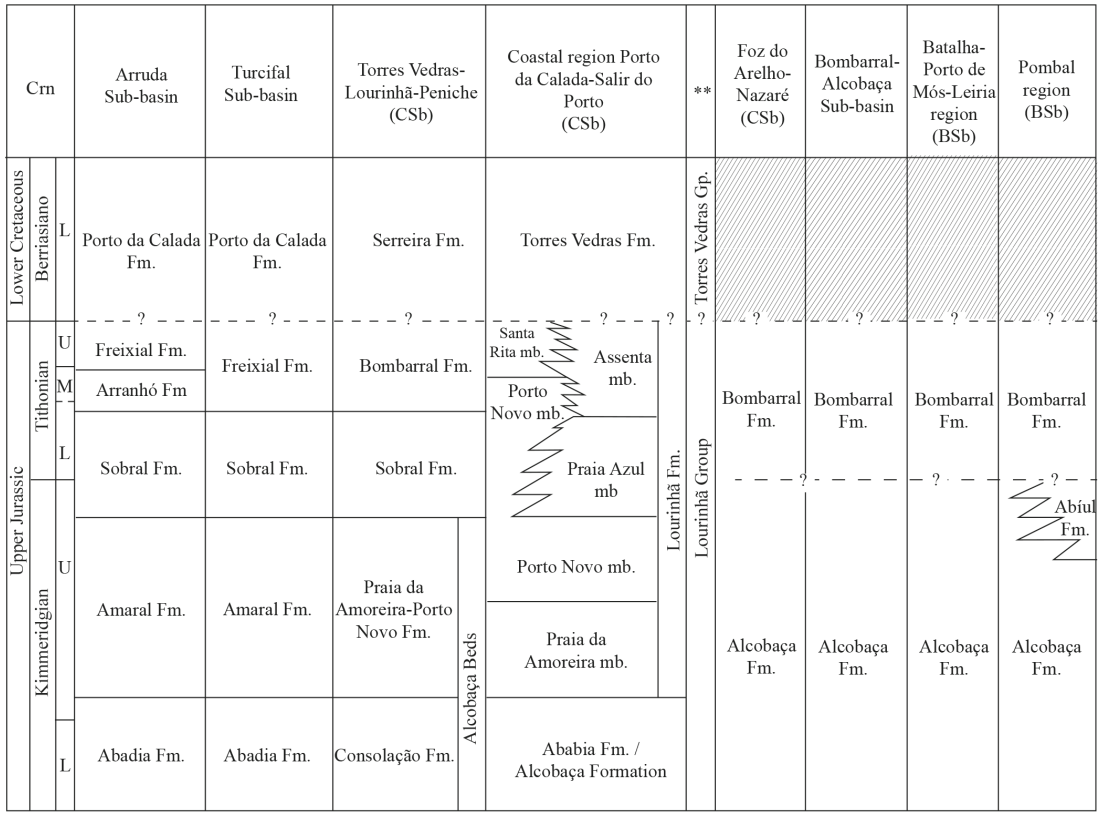


Figure 5.2. Stratigraphic correlation between the nomenclature proposed for *i*) Turcifal Sub-basin (based on Pereda-Suberbiola et al., 2005, Kullberg et al., 2006, Schneider et al., 2009), *ii*) Arruda Sub-basin (Kullberg et al., 2006); *iii*) Consolação Sub-basin areas: Torres Vedras-Lourinhã-Peniche (based on Manuppella et al., 1999), Foz do Arelho-Nazaré coastal sector (Kullberg et al., 2006; Azerêdo et al., 2010); *iv*) Bombarral-Alcobaça Sub-basin (based on Azerêdo et al., 2010); *v*) Batalha-Leiria region (based on Manuppella et al., 2000; Kullberg et al., 2006; Escaso et al., 2007) and *vi*) Pombal region (Kullberg et al., 2006; Malafaia et al., 2010). The stratigraphy proposed by Hill (1988) for the coastal sector from Porto da Calada to Salir do Porto is also plotted. Crn – Chronostratigraphy; ***sensu* Yagüe et al. 2006. BSb, Bombarral Sub-basin (following Kullberg et al., 2006); CSb, Consolação Sub-Basin (following Taylor et al., 2013).

5.3. INSTITUTIONAL ABBREVIATIONS

MG, Museu Geológico do Laboratório Nacional de Energia e Geologia, Lisbon, Portugal; NHMUK, Natural History Museum, London, UK; SHN, Sociedade de História Natural, Torres Vedras, Portugal (plus (JJS) for the José Joaquim collection deposited in the Sociedade de História Natural).

5.4. SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842
Saurischia Seeley, 1887
Sauropodomorpha Huene, 1932
Sauropoda Marsh, 1878

5.4.1. Albergaria dos Doze

Material: Middle to posterior caudal vertebra (MG 4811).

Locality: The precise locality and formation from which the vertebra comes is unknown. Lapparent and Zbyszewski (1957) referred that this vertebra come from Albergaria dos Doze, 250m N45-W from the S. José Chapel (in the railway). In Albergaria dos Doze the present railway intersect Cretaceous sediments, "*Cenomaniano inferior, Albiano, Aptiano, Neocomiano*", nevertheless the referred point is close to the river Arunca, which intersect Upper Jurassic sediments of "*Complexo Vale de Lagares*" (Teixeira et al., 1966) that corresponds to the Alcobaça Formation, Kimmeridgian to basal Tithonian (Kullberg et al., 2006). The stratigraphy of this area is uncertain, and the Upper Jurassic sediments outcropping in the Albergaria dos Doze might correspond to Bombarral Fm. (e.g. Malafaia et al., 2010). In this work, we consider the age for this vertebra as uncertain.

Description: Middle to posterior caudal vertebra lacking the neural arch (Fig. 5.3a.I-a.VI). The centrum is cylindrical, with a marked longitudinal crest on the lateral face. The centrum bears an amphicoelous condition, concave anterior and posterior articular facets. The posterior articulation is slightly compressed dorsoventrally. The ventral face is convex-to-flat, having smooth ventrolateral crests associated to the articulations for chevrons. The posterior articulations are more developed than the anterior ones, and both present a semi-elliptical outline. The neural arch is placed at midpoint of the dorsal surface centrum with a slight anterior displacement.

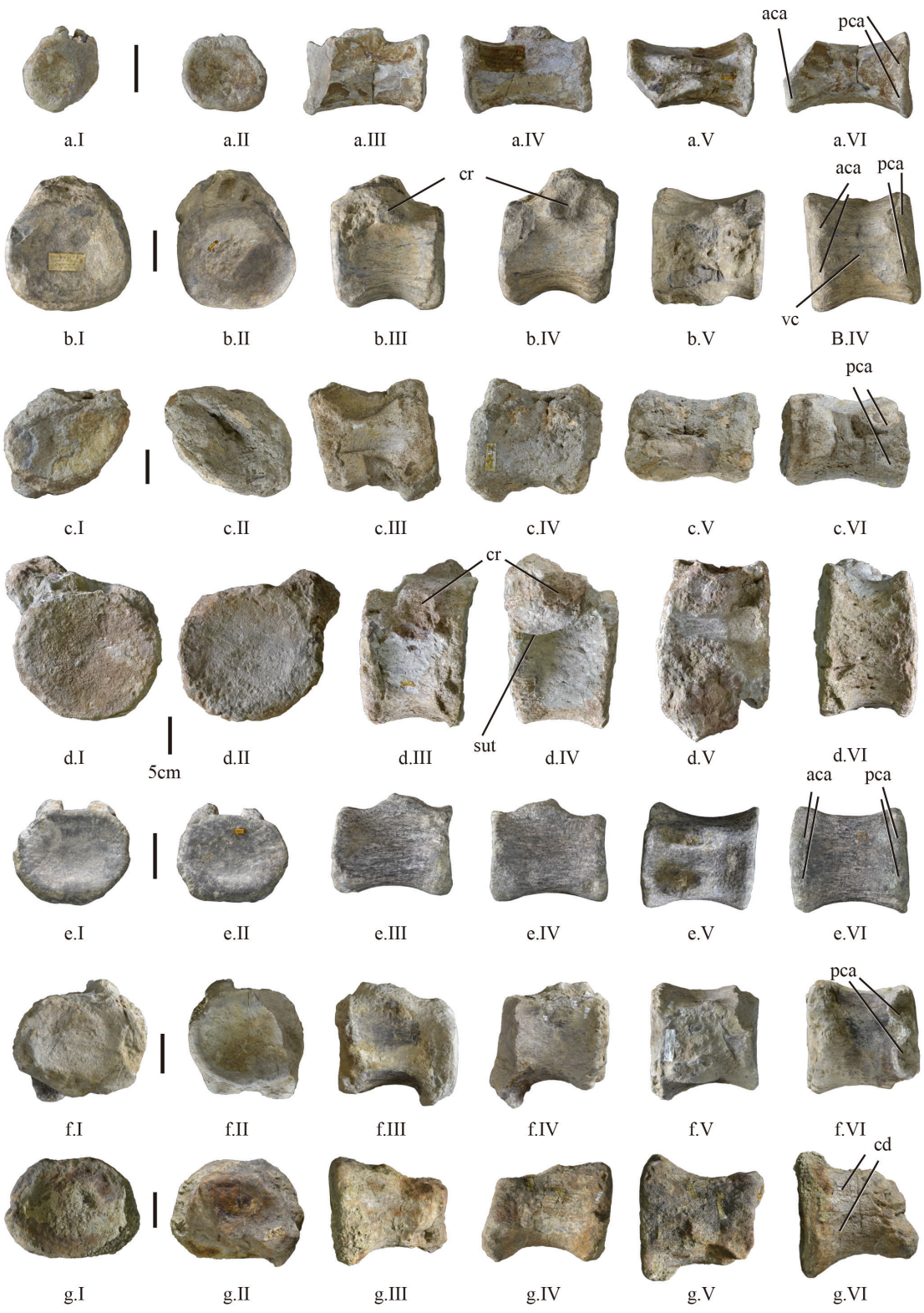
Discussion: MG 4811 was firstly related to *Megalosaurus pombali* by Lapparent and Zbyszewski (1957). This taxon was considered *nomina dubia* by Antunes and Mateus (2003). Mateus (2005) referred this caudal vertebra to an indeterminate theropod. An anteroposteriorly short neural arch, seems to exclude this caudal vertebra to Theropoda, and its general morphology resembling better the morphology of the middle and posterior caudal vertebrae of sauropods. This middle/posterior caudal vertebra bears some features that could help to discriminate from some morphotypes present in the Iberian Upper Jurassic. This vertebra can be differentiated from the most middle posterior caudal vertebrae of *Lusotitan* and *Galveosaurus* (Barco, 2009; Mannion et al., 2013), by the presence of a well-developed amphicoelous centrum, a neural arch placed at midpoint of the centrum dorsal surface, and not marked dorsoventrally compressed centrum. In *Aragosaurus* (Sanz et al., 1987; Royo-Torres et al., 2014) the articulations are slightly flatter and the lateral faces do not bears longitudinal crests as in MG 4811. The position of the neural arch at midpoint of the centrum differs from that of Titanosauriformes in which the neural arch is anteriorly displaced (e.g. Salgado et al., 1997; D'Emic, 2012). The vertebra is also excluded from Diplodocinae by the absence of several features such as a lateral fossa, a transversely concave ventral face, a marked ventrolateral crests or a quadrangular cross-section (e.g. Wilson, 2002; Whitlock, 2011). *Lourinhasaurus*, *Turiasaurus*, *Losillasaurus* and *Zby* do not preserved middle caudal vertebra (Casanovas et al., 2001; Royo-Torres et al., 2006; Mateus et al., 2014; Mocho et al., 2014a). In the absence of diagnostic features, this vertebra is considered here as Sauropoda indet.

5.4.2. Atalaia

Material: Three dorsal vertebra fragments (MG 8809) including a transverse process and a partial neural arch preserving the prezygapophyses.

Locality and horizon: Atalaia (Lourinhã), Sobral Formation (Manuppella et al., 1999).

Description: Three so far unpublished fragments of neurapophysis from Atalaia are described (Fig. 5.4). One of those fragments corresponds to the prezygapophyses and parapophyses of a middle or posterior dorsal vertebra. The prezygapophysis is transversely compressed and bears a flat surface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supported by a simple and dorsally unbifurcated centroprezygapophyseal lamina (cprl). The prezygapophysis is linked with a rough parapophyses by a prezygoparapophyseal lamina (prpl) interrupted at midlength. The parapophyses is supported by a simple anterior centroparapophyseal lamina (acpl). The other neural arch fragment is a poorly preserved transverse process. This transverse process culminates in a subrectangular diapophysis, with a rough and concave surface. From the diapophysis parts three marked laminae: *i*) a ventral one, the posterior centroparapophyseal lamina (pcpl), posteriorly directed; *ii*) a subhorizontal and posterior one, the postzygadiapophyseal lamina (podl); and *iii*) a subhorizontal and anterior one, the prezygadiapophyseal lamina (prdl). The dorsal surface of the transverse process is flat near the diapophysis but a deep fossa appears medially to this flat area. The distal end of the transverse process curves smoothly into the dorsal surface of the process.

Discussion: These fragments come from the same locality of the *Lusotitan atalaiensis* lectotype, and the state of preservation is similar. Furthermore, they seem to represent individuals with similar sizes. Nevertheless, no information allows relating these fragments to the same fossil site. The presence of an acpl is common in almost all middle and posterior dorsal vertebrae of sauropods (e.g. Wilson, 2002; Carballido and Sander, 2014), as well as the other set of observed laminae: cprl, pcdl, podl and prdl (e.g. Wilson, 1999; Upchurch et al., 2004). At the moment, these fragments have to be assigned to an indeterminate sauropod.

5.4.3. Porto das Barcas

Material: Middle caudal vertebra (MG 8805).

Locality and horizon: Porto das Barcas (Lourinhã), Sobral Formation, upper Kimmeridgian-basal Tithonian (Fürsich, 1981; Manuppella et al., 1999; Kullberg et al., 2006; field observ., PM).

Description: MG 8805 is a middle caudal vertebra transversely deformed (Fig. 5.3c.I-c.VI). The neural arch is placed at midpoint of the centrum. The anterior and the posterior articular facets are concave. A longitudinal crest could be recognized in the lateral face above midheight of the centrum. Posterior ventrolateral crests are also present and associated to the chevron posterior articular facets. The posterior facets for the chevrons are semicircular. The anterior ventral border is not preserved, being impossible to verify the presence of anterior facets for the chevrons. The ventral face is transversaly convex.

Discussion: This vertebra was firstly related to *Apatosaurus alenquerensis* (Lapparent and Zbyszewski, 1957, pg. 38). Antunes and Mateus (2003) and Mateus (2005, p.86; referred as MG 8800) attributed these vertebrae to *Lourinhasaurus alenquerensis*. The position at midpoint of the centrum excluded it of Titanosauriformes clade, featured by anteriorly displaced neural arches (e.g. Salgado et al., 1997; D'Emic, 2012). No more features are present to propose a more precise position within Sauropoda, and it should be considered as an indeterminate sauropod.

Figure 5.3. Sauropod caudal vertebra of the Museu Geológico. Sauropoda indet., middle or posterior caudal vertebra (MG 4811) in anterior (a.I), posterior (a.II), left (a.III), right (a.IV), dorsal (a.V) and ventral (a.VI) views. Sauropoda indet., anterior caudal vertebra (MG 4804) in anterior (b.I), posterior (b.II), left (b.III), right (b.IV), dorsal (b.V) and ventral (b.VI) views. Sauropoda indet., middle caudal vertebra (MG 8805) in anterior (c.I), posterior (c.II), left (c.III), right (c.IV), dorsal (c.V) and ventral (c.VI) views. Sauropoda indet., anterior caudal vertebra (MG 4800) in anterior (d.I), posterior (d.II), left (d.III), right (d.IV), dorsal (d.V) and ventral (d.VI) views. Sauropoda indet., middle caudal vertebra (MG 4802) in anterior (e.I), posterior (e.II), left (e.III), right (e.IV), dorsal (e.V) and ventral (e.VI) views. Eusauropoda indet., middle caudal vertebra (MG 8800) in anterior (f.I), posterior (f.II), left (f.III), right (f.IV), dorsal (f.V) and ventral (f.VI) views. Cf. *Lusotitan atalaiensis*, middle caudal vertebra (MG 8804) in anterior (g.I), posterior (g.II), left (g.III), right (g.IV), dorsal (g.V) and ventral (g.VI) views. Scale bar: 5cm.

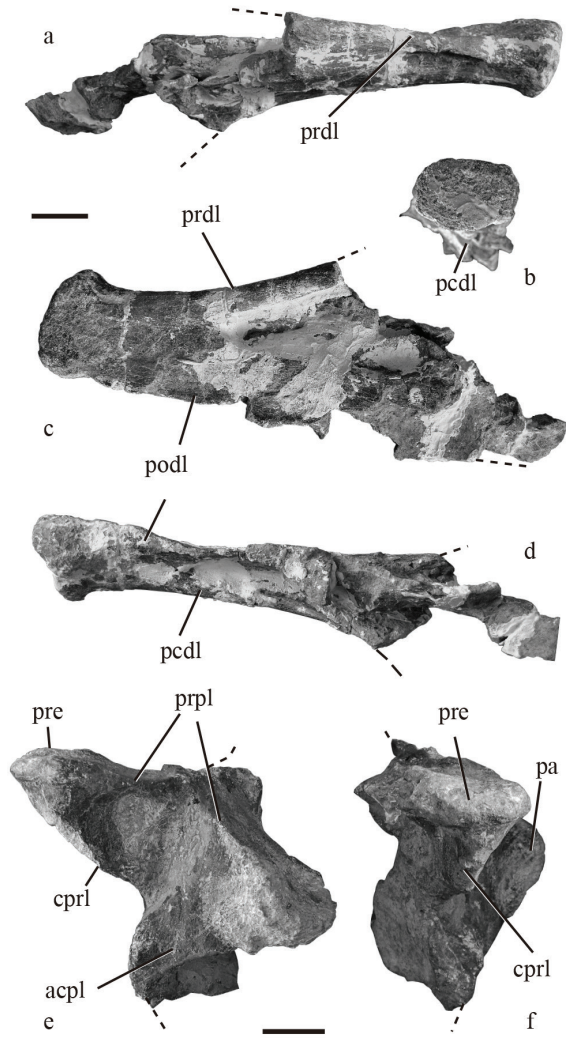

Figure 5.4. Sauropoda indet., middle or posterior dorsal neural arch fragments from Atalaia (MG 8809). Left transverse process in anterior (a), lateral (b), dorsal (c) and posterior (d) views. Partial neural arch in lateral (e) and anterior (f) views. Scale bar: 5cm

5.4.4. Porto Novo

Material: Anterior caudal vertebra (MG 4800).

Locality and horizon: Porto Novo (Maceira, Torres Vedras), Praia da Amoreira-Porto Novo Formation, upper Kimmeridgian-to-basal Tithonian (Manuppella et al., 1999).

Description: This vertebra probably corresponds to a subadult individual because the neural arch and caudal ribs are not fully fused (Fig. 5.3d.I-d.VI). The facets for the chevrons are rudimentary near the anterior articulation and absent near the posterior border. The caudal ribs are dorsoventrally deep. These two features (deep caudal ribs and the presence of rudimentary chevron articulations) suggests that this vertebra corresponds to one of the most proximal vertebrae of the tail. The vertebra is anteroposteriorly short and subcircular in anterior view, with a slight dorsoventral compression. The anterior and posterior articular faces are concave, the anterior more concave than the posterior

one. The ventral face is flat to convex and a slight longitudinal crest are present, probably related with the articulations for the chevrons. The neural arch is anteriorly displaced. The lateral face is convex and a fossa or pleurocoel are absent.

Discussion: MG 4800 was firstly related to *Brachiosaurus atalaiensis* (Lapparent and Zbyszewski, 1957, pl. XXVI, 94), to *Lusotitan atalaiensis* by Antunes and Mateus (2003) and to *Lourinhasaurus alenquerensis* by Mateus (2005). The most anterior preserved centrum of *Lourinhasaurus* occupies a position in the caudal series between 3rd and 8th (Mocho et al., 2014a). Presence of deeper caudal ribs suggests that MG 4800 is probably anterior than preserved vertebrae of *Lourinhasaurus*. Porto Novo vertebra is amphicoelous, differing from the condition observed in *Lourinhasaurus* that has vertebrae with flat posterior face, bearing a central smooth concavity (Mocho et al., 2014a). One of the proposed autapomorphies for this taxon is the presence of a circular spinoprezygapophyseal fossa (sprf) on the anterior caudal vertebra, also described in *Jobaria* (Sereno et al., 1999). Nevertheless, the absence of the neural arch in MG 4800 does not allow testing the presence of this feature. *Lusotitan atalaiensis* is also distinguished from MG 4800 by the presence of a flat posterior articular face (Mannion et al., 2013). *Aragosaurus ischiaticus*, present a flat-to-concave posterior face (Royo-Torres et al., 2014) resembling the condition present in MG 4800. At the moment, we consider that this vertebra does not present any significant feature in order to propose a more accurate systematic approach, and we prefer to attribute it to an indeterminate sauropod.

5.4.5. Praia de Santa Cruz

Material: Middle caudal vertebra (MG 4802).

Locality and horizon: Alto da Vela (Torres Vedras). Alto da Vela is South of Praia de Santa Cruz where outcrops the Praia de Amoreira-Porto Novo Formation, upper Kimmeridgian-to-basal Tithonian in age (Manuppella et al., 1999).

Description: Partial middle caudal vertebra lacking the neural arch (Fig. 5.3e.I-e.VI). The lateral face of this vertebra lacks any crests. The ventral face is convex to flat. The anterior and posterior articulations are concave and dorsoventrally compressed. In the ventral face there are semicircular facets for the chevron articulation near the posterior and anterior articulations. The outline of the articular faces of the centrum is eroded, but is possible to verify that posterior facets for chevron are more developed than the anterior ones. No pleurocoels or fossae are present in the lateral and ventral faces of MG 4802.

Discussion: Lapparent and Zbyszewski (1957) assigned this vertebra to *Apatosaurus alenquerensis*. Antunes and Mateus (2003) and Mateus (2005) related MG 4802 (labelled as MG 4804 by Mateus, 2005) to *Lourinhasurus alenquerensis*. However, is not possible to compare MG 4802 with *Lourinhasaurus alenquerensis* by the absence of middle caudal vertebrae in the latter (Lapparent and Zbyszewski, 1957; Mocho et al., 2014a).

This middle caudal vertebra bears a slight anterior displacement of the neural arch. A marked anterior displacement of the neural arch in anterior and middle caudals is considered a synapomorphy of Titanosauriformes (Salgado et al., 1997; Upchurch et al., 2004; D'Emic, 2012). Several taxa outside Titanosauriformes can present only a slight displacement on the neural arch on middle caudal vertebrae (Osborn and Mook, 1921; Janensch, 1929; McIntosh et al., 1996b) different from the marked anterior displacement present in the basal eusauropod *Cetiosaurus* (Upchurch and Martin, 2003) and titanosauriforms (e.g. Gomani, 2005; Rose, 2007; Gonzalez-Riga, 2009; D'Emic, 2013; Mannion et al., 2013) or *Galveosaurus*.

This vertebra is not so dorsoventrally compressed as in *Lusotitan* (Mannion et al., 2013) and does not bear any circular smooth concavities on the ventral face as occur in the former taxon (pers. observ., PM). *Lusotitan* also bears two other features that allow distinguishing MG 4802

from this taxon: the presence of transverse pits on the articulations and flat posterior articulations of the posterior middle caudal centra (Lapparent and Zbyszewski, 1957; Mannion et al., 2013). MG 4802 presents a morphology similar to that of *Aragosaurus* (Sanz et al., 1987; Royo-Torres et al., 2014), but they do not share apomorphic features.

In conclusion, no remarkable features are present in order to obtain a more accurate taxonomic determination of MG 4802, and for the moment, should be considered as an indeterminate sauropod.

5.4.6. Praia das Almoinhas?

Material: Posterior caudal vertebra (MG 8799).

Locality and horizon: The label associated to this bone refers it, with doubt, to the Praia das Almoinhas locality, and no references about this locality were found. Mateus (2005) suggested two possible localities for this vertebra: *i*) Casais do Almoinha close to Salir de Matos and where outcrops the Bombarral Formation, Tithonian in age (Kullberg et al., 2006; Azerêdo et al., 2010), and *ii*) the Vale Almoinha close to Cambelas (Torres Vedras) where outcrops the Freixial Fm., Tithonian in age (Pereda-Suberbiola et al., 2005; Kullberg et al., 2006).

Description: MG 8799 is a posterior fragment of the centrum of a posterior caudal vertebra that preserves part of the neural arch pedicels (Fig. 5.5a-d). The posterior articular face is generally flat, bearing a central concavity. The dorsal margin of the posterior face has two semicircular projections. The lateral face bears a longitudinal crest at midheight. The ventral face bears near the posterior articulation two semi-circular-to-circular articulations for the chevrons. From these facets parts two smooth ridges that limit a transverse concave region that disappears anteriorly by the smoothing of the ventral crests. Anterior to these crest the ventral face is flat. The centrum has a diamond-shaped cross-section.

Discussion: It is not possible to determinate the relative position of the neural arch and two scenarios, with different implications, can be posed. If the neural arch has a central position, the centrum should be appreciable longer, with at least four times the dorsoventral width of the posterior articulation, particular longer for a non-diplodocid (see Wilson, 2002; Upchurch et al.,

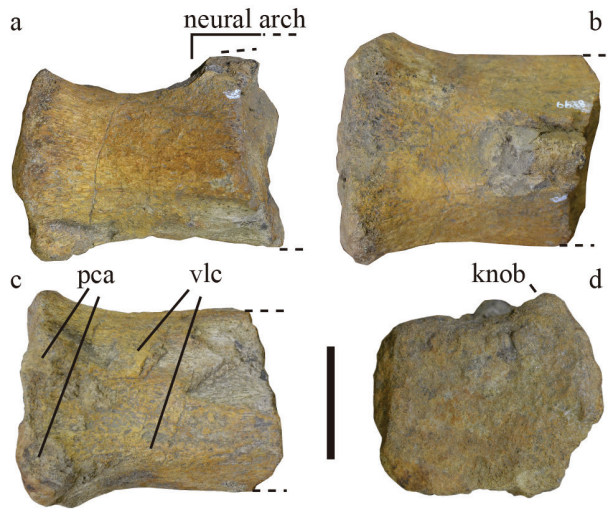

Figure 5.5. Sauropoda indet, posterior caudal vertebra from Praia de Almoinhas (MG 8799) in right (a), dorsal (b), ventral (c) and posterior (d) views. Scale bar: 5cm

2004; Whitlock, 2011). If not, the neural arch should present in an anterior position, synapomorphy of Titanosauriforms (e.g. Upchurch et al., 2004) and convergent with *Cetiosaurus oxoniensis* (Upchurch and Martin, 2003). Nevertheless, the posterior vertebrae of *Cetiosaurus* bears concave posterior articular faces. A slight transverse concavity is observed in the ventral surface of MG 8799, bordered by smooth ventrolateral ridges. Similar ridges are also observed in a posterior caudal vertebra referred to *Europasaurus* (DFMMh/FV 995, pers. observ., PM). Transverse concave ventral faces in middle caudal vertebrae are also present in diplodocids (Osborn, 1904; McIntosh, 2005; Remes, 2006) and in some titanosaurs such saltasaurids (Upchurch et al., 2004; Wilson, 2002), nevertheless, this concavity is much more developed than in MG 8799, as occur in MG 4819, 4821, 4826, also described in this study. At the moment, this vertebra is considered as an indeterminate sauropod.

Eusauropoda Upchurch, 1995
Eusauropoda indet.

5.4.7. Salir de Matos

Material: Anterior caudal vertebra (MG 4804).

Locality and horizon: Salir de Matos (Caldas da Rainha), Bombarral Formation, dated to Tithonian (Manuppella et al., 1999; Azerêdo et al., 2010).

Description: This vertebra is probably one of the last anterior vertebra because the presence of a reduced caudal ribs (Fig. 5.3b.I-b.VI). Anterior and posterior articulations are concave and bear a subcircular outline, with a slight dorsoventral compression. The neural arch is located in the anterior part of the centrum. In the ventral face, there are semicircular chevron articulations near the anterior and posterior articulation of the centrum, being the posterior ones more developed. From the chevrons articulations start smooth longitudinal crests that never reach the midpoint of the centrum. These crests are different from the marked lateroventral crests present in diplodocids (e.g. Osborn, 1896; McIntosh, 2005; Remes, 2006). Between these not pronounced lateroventral crests there is a sagittal smooth crest at the midpoint of centrum. Not taking into account this sagittal crest, the ventral face is convex at midpoint. The lateral face lacks fossae or pleurocoels and bear a longitudinal crest close to the transition between the ventral and lateral face.

Discussion: This vertebra was firstly related to *Apatosaurus alenquerensis* by Lapparent and Zbyszewski (1957). Dantas et al. (1998) established a new genus for this species, *Lourinhasaurus*, currently based on Moinho do Carmo specimen (Mocho et al., 2014a) defined as its lectotype (Antunes and Mateus, 2003). This vertebra was related to this taxon by Antunes and Mateus (2003) and to cf. *Lourinhasaurus alenquerensis* by Mateus (2005), however, this taxonomic attribution could not be supported by the impossibility to compare it with *Lourinhasaurus* due the absence of posterior anterior caudal vertebrae attributed to this taxon (Mocho et al., 2014a).

Salgado et al. (1997) or D'Emic (2012) considered as a diagnostic feature of Titanosauriformes the anterior position of the neural arch in the anterior and middle caudal vertebrae. Nevertheless, anteriorly displaced neural arches in the anterior caudals have a wider distribution within Sauropoda (Hatcher, 1901; Osborn and Mook, 1921; Ostrom and McIntosh, 1966; McIntosh et al., 1996a, b; Casanovas et al., 2001; Ouyang and Ye, 2002; Upchurch and Martin, 2003; Allain and Aquesbi, 2008; Remes et al., 2009; Royo-Torres and Upchurch, 2012). This condition is so far exclusive of Titanosauriformes only when is referred to the last proximal and middle caudal vertebrae (see Mocho et al., 2014a). Having an isolated caudal vertebra, its attribution to Titanosauriformes is not very robust. *Cetiosaurus oxoniensis* Phillips, 1871, for example, is a basal eusauropod having anteriorly displaced neural arch in anterior and middle caudal vertebrae (Upchurch and Martin, 2003). Consequently, MG 4804 should be attributed to

an indeterminate eusauropod. The presence of a smooth sagittal ventral crest is shared with the tail collected in São Bernardino (MG 4978) that will be described below in detail. The absence of pleurocoels, ventrolateral crests or a transversely concave ventral face differentiate this vertebra from that of the Diplodocidae (see Hatcher, 1901; Osborn, 1904; Lull, 1919; McIntosh, 2005; Remes, 2006).

5.4.8. Foz do Arelho

Material: Bifurcated neural spine of a posterior cervical or anterior dorsal vertebra (MG 4920).

Locality and horizon: Monte da Cruz do Facho, Foz do Arelho (Caldas da Rainha), Bombarral Formation, Tithonian in age (Manuppella et al., 1999; Kullberg et al., 2006; Azerêdo et al., 2010).

Description: A partial bifurcated neural spine was collected from Foz do Arelho (MG 4920, Fig. 5.6). This neural spine preserves part of the postzygapophyses, and lacks the prezygapophyses and the prespinal process. The posterior face of this neural spine is not prepared. In comparison with bifurcated neural spines of presacral vertebrae in other sauropods (e.g. Hatcher, 1901; Osborn and Mook, 1921; Janensch, 1929; Gilmore, 1936; Ostrom and McIntoch, 1966; Ouyang and Ye, 2002; Royo-Torres et al., 2006; Wilson and Upchurch, 2009), this neural arch probably belongs to a posterior cervical or an anterior dorsal vertebra since its morphology fit with that of transitional vertebrae between the cervical and dorsal series. This neural spine is not bifurcated up to the base of the neural spine (at postzygapophyses level) as occur in the first dorsal vertebrae of *Apatosaurus* (Gilmore, 1936) in the last cervicals and first dorsals of *Camarasaurus* (Osborn and Mook, 1921). Several laminae are recognized. From the postzygapophyses parts two laminae. One of them is interpreted as a single lateral spinopostzygapohyseal lamina (lat. spol, but it is not possible to confirm the presence of a medial spol), which diverge ventrally. On the postzgapophyses part of the podl is preserved. Two spinodiapophyseal laminae are recognized: short posterior spinodiapophyseal laminae (post. spdl) in connection with a triangular process, and incomplete anterior spinodiapophyseal laminae (ant. spdl) longer than the post. spdl. Part of the spinoprezygapophyseal laminae are also preserved. No median tuberculum is observed, but the state of preservation does not exclude the possibility to be present in this vertebra. The broken base of the neural arch reveal some internal camera.

Discussion: According with several published phylogenetic approaches (e.g. Wilson, 2002; Upchurch et al., 2004; Harris, 2006; Mannion et al., 2013; Carballido and Sander, 2014), the development of bifurcated neural spines occurred several times along the evolutionary history of eusauropods. Bifurcated neural spines in the transition of the cervical and dorsal series is recorder in the basal eusauropods *Turiasaurus* (Royo-Torres et al., 2012; pers observ., R. R-T) and *Mamenchisaurus* (Ouyang and Ye, 2002); and in the flagellicaudatans *Dicraeosaurus* (Janensch, 1929), *Amargasaurus* (Salgado and Bonaparte, 1991), *Diplodocus* (Hatcher, 1901), *Apatosaurus* (Gilmore, 1936), *Barosaurus* (Lull, 1919) and *Supersaurus* (Lovelace et al., 2007). Within Macronaria, bifurcated neural spines on this sector of the presacral series also occur in *Camarasaurus* (e.g. Osborn and Mook, 1921) and in Euhelopodidae (Suteethorn et al., 2009; Wilson and Upchurch, 2009; D'Emic, 2012; D'Emic et al., 2013). The presence of bifurcated neural spines is apparently restricted to Eusauropoda clade, suggesting the placement of MG 4920 within this clade. The presence of ant. spdl and post.spdl is a common feature within sauropods (Wilson, 2012) and suggests that this neural spine is probably from an anterior dorsal vertebra (following Wilson, 1999). An incipient triangular aliform process is interpreted in MG 4920. This feature is shared with *Camarasaurus* (Osborn and Mook, 1921) but not with Flagellicaudata (Hatcher, 1901; Lull, 1919; Janensch, 1929; Gilmore, 1936; Salgado and Bonaparte, 1991; Lovelace et al., 2007) and Euhelopodidae (Suteethorn et al., 2006; Wilson and Upchurch, 2009; D'Emic, 2012; D'Emic et al., 2013). The presence of bifurcated neural spines in the Portuguese Upper Jurassic sauropods is just described for *Lourinhasaurus*. Mocho et al. (2014a)

described a middle dorsal neural spine with a dorsal recess similar to that of *Camarasaurus* (Osborn and Mook, 1921) suggesting the possibility of bifurcated neural spines in more anterior vertebrae.

On the other hand, *Dinheirosaurus* is a diplodocid supposedly featured by unbifurcated and transversely compressed dorsal neural spines (Bonaparte and Mateus, 1999; Mannion et al., 2012). Nevertheless, we assume a more caution position considering the presence of unbifurcated neural spines as unknown (following Whitlock, 2011). We consider that it is not possible to test the presence of unbifurcated neural spines in the *Dinheirosaurus* holotype up to the full preparation of the specimen. Up to found more material, we consider that MG 4920 represents an indeterminate eusauropod.

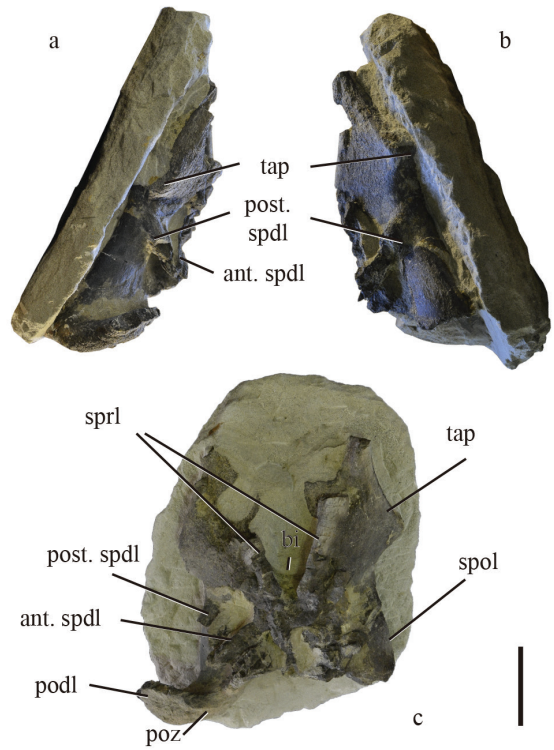

Figure 5.6. Eusauropoda indet., partial posterior cervical or anterior dorsal neural arch from Foz do Arelho (MG 4920) in right (a), left (b) and anterior view. Scale bar: 10cm

5.4.9. Porto das Barcas II

Material: Middle caudal vertebra (MG 8800).

Locality and horizon: Porto das Barcas (Lourinhã), Sobral Formation, upper Kimmeridgian-basal Tithonian (Fürsich, 1981; Manuppella et al., 1999; Kullberg et al., 2006; field observations, PM).

Description: MG 8800 is a partial middle caudal vertebra lacking its neural arch (Fig. 5.3f.I-f.VI). The anterior and posterior articular faces are concave and dorsoventrally compressed. The base of the neural spine is slightly displaced anteriorly. The lateral face bears a longitudinal crest slightly displaced ventrally (this crest is very close to the transition between the lateral and the ventral faces). The ventral surface of the centrum is convex-to-flat. The posterior articular facets for the chevrons are semicircular, well developed and concave. In lateral view, they are appreciable ventrally projected. The anterior facets for the chevrons are not present, probably due to some erosion of the anterior border.

Discussion: This vertebra was firstly assigned to *Apatosaurus alenquerensis* (Lapparent and Zbyszewski, 1957, pg. 38, pl. XVIII, fig. 49). Antunes and Mateus (2003) and Mateus (2005) attributed it to *Lourinhasaurus alenquerensis*. However, the absence of middle caudal vertebrae in *Lourinhasaurus* lectotype does not allow testing this attribution. MG 8800 present dorsoventral compression similar to *Lusotitan atalaiensis* (Lapparent and Zbyszewski, 1957; Mannion et al., 2013) or *Galveosaurus* (Barco, 2009). Dorsoventral compressed centra are common in basal titanosauriforms (Janensch, 1950; Tidwell et al., 1999, 2001; Upchurch et al., 2004; Canudo et al., 2008; Royo-Torres, 2009), and also occur in some basal eusauropods (Upchurch and Martin, 2003). This vertebra also presents a slight anterior position of the neural arch, but it is not so marked as in titanosauriforms (e.g. Salgado et al., 1997; Wilson, 2002; Upchurch et al.,2004; D'Emic, 2012), or in the basal eusauropod *Cetiosaurus oxoniensis* (Upchurch and Martin, 2003). This vertebra does not share with the Diplocinae a transversely concave ventral surface or lateral pneumaticity (Wilson, 2002; Whitlock, 2011). Dorsoventral compressed anterior and middle centra are absent in basal sauropods (e.g. Cooper, 1984; Yadagiri, 2001; Rauhut, 2003; Allain and Aquesbi, 2008; Bandyopadhyay et al., 2010; McPhee et al., 2014). MG 8800 is fragmentary, but the presence of dorsoventrally compressed centrum is a feature just present in basal titanosauriforms and some eusauropods (e.g. Upchurch and Martin, 2003; Upchurch et al., 2004), suggesting that this sauropod is a member of Eusauropoda.

5.4.10. São Bernardino

Material: Partial tail composed by 15 anterior to middle caudal vertebrae (MG 4978).

Locality and horizon: São Bernardino (Peniche), Praia de Amoreira-Porto Novo Formation, upper Kimmeridgian-basal Tithonian in age (Manuppella et al., 1999).

Description: This partial tail is composed by 15 centra from the anterior-to-middle sector (Figs. 5.7, 5.8). Here we describe the existing caudal vertebrae as CdA-O. Almost all the centra lack the neural arches with the exception of CdG and CdO that preserve part of neural arch pedicels. The preserved centra present some oblique deformation. Regardless the deformation, it is interpreted that the anterior centra have an original slight dorsoventral compression. In anterior/posterior view, they have a hexagonal outline. The anterior centra are amphicoelous, with concave anterior and posterior articular faces. The posterior face becomes progressively flat toward the anterior part of the series. The ventral face is transversely narrow, becoming wider in more posterior centra. These vertebrae presents a longitudinal and sagittal smooth crest that are present up to CdE (on the anterior half of the ventral face) and reappear in CdK-to-CdM.

The anterior caudal vertebrae bear dorsoventrally and transversely short caudal ribs that are posterolaterally oriented. In anterior view, the caudal ribs are laterally directed with a slight dorsal projection that can be related with deformation. Short and rudimentary caudal ribs suggest that these vertebrae are the most posterior anterior caudal vertebrae. The caudal ribs are present up to the CdF, considered here as the last anterior centra. Sauropods generally present up to 10 (in titanosaurs) to 20 (in most basal sauropods) caudal vertebrae with caudal ribs (e.g. Wilson and Sereno, 1998; Wilson, 2002). Eusauropods non-titanosaurs present around 15 caudal vertebrae with caudal ribs. Assuming the presence of at least 15 caudal vertebrae with caudal ribs in the São Bernardino sauropod, the anterior most nine caudal vertebrae are not preserved.

In CdB, just below the caudal rib, there is a longitudinal crest on the lateral face. This longitudinal crest moves to a more ventral position along the caudal series. In CdC, CdD and CdE, in the point where the crest touch the posterior and anterior articulation appears a lateral projection that progress slightly to the lateral face. In middle caudal vertebrae these crests become less pronounced. In CdF, there is another longitudinal crest on the lateral surface of the centrum near the region of the caudal rib (the last caudal rib of the series). This crest keeps this position up

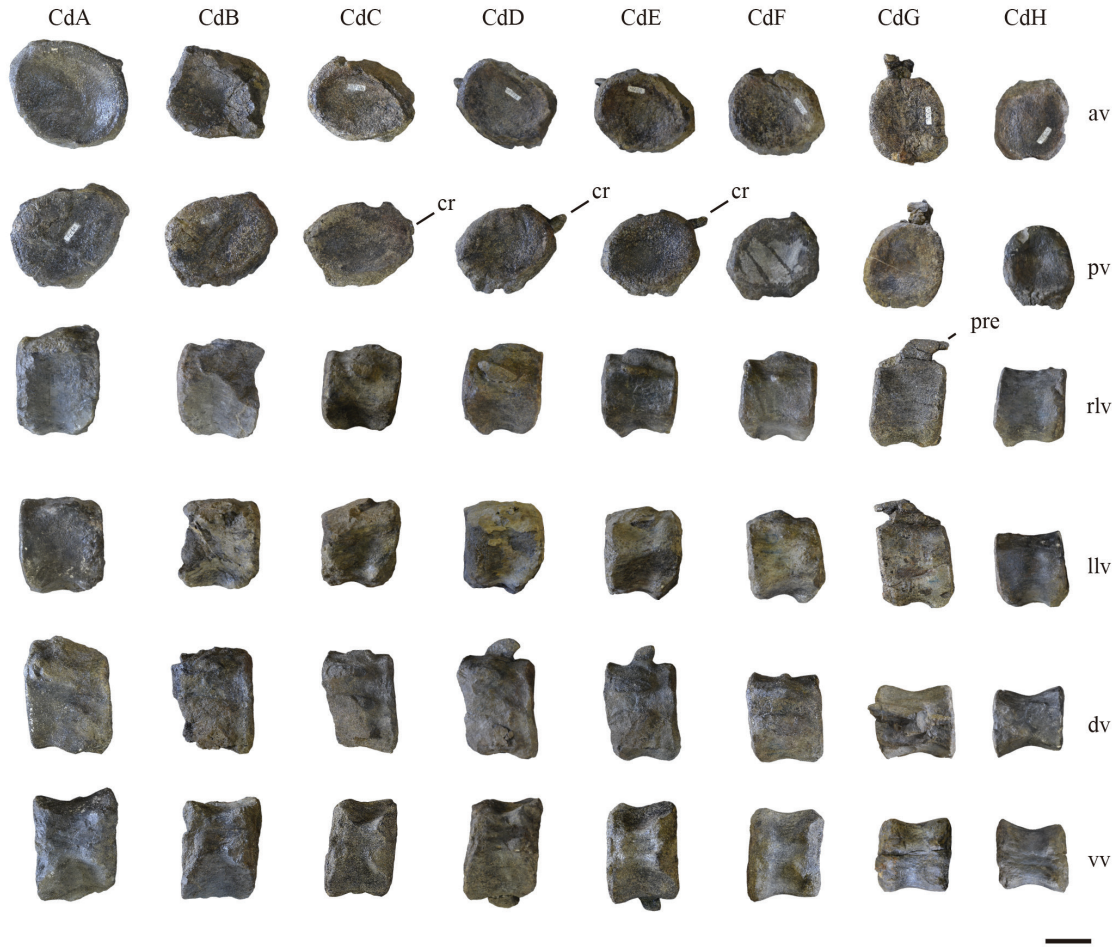

Figure 5.7. Eusauropoda indet., partia caudal series from São Bernardino. Caudal vertebrae from CdA to CdH in anterior (av), posterior (pv), right (rv), left (lv), dorsal (dv) and ventral (vv) views. Scale bar: 10cm.

to the last preserved caudal centrum. The articular facets for the chevrons are semicircular, being the posterior ones more pronounced. Between CdD and CdJ the articular facets for the chevrons bear a marked anteroventral projection. Short and smooth longitudinal crests start from these articulations. The anterior preserved caudal vertebrae lack the neural arch, but they are clearly placed in the anterior half of the centrum, a common situation in most anterior caudal vertebrae of sauropods (Mocho et al., 2014a).

The centra of middle caudal vertebrae (from the CdG) are almost subcircular in anterior/posterior view, and in some cases, the dorsoventral width could be higher than the transverse width (e.g. CdG or CdH). The last preserved centra have a slight dorsoventral compression. The centra are amphicoelous. The ventral face is generally flat-to-convex and presents a smooth sagittal crest up to CdM, as occurs in the anterior caudal vertebrae. From the CdI up to the last preserved centrum, the posterior face becomes less concave, suggesting that the posterior face might acquire a flat articulation in the posterior caudal vertebrae as in *Lusotitan atalaiensis* (Mannion et al., 2013). The neural arch is slightly displaced to the anterior half of the centrum, but do not touch the anterior articulation.

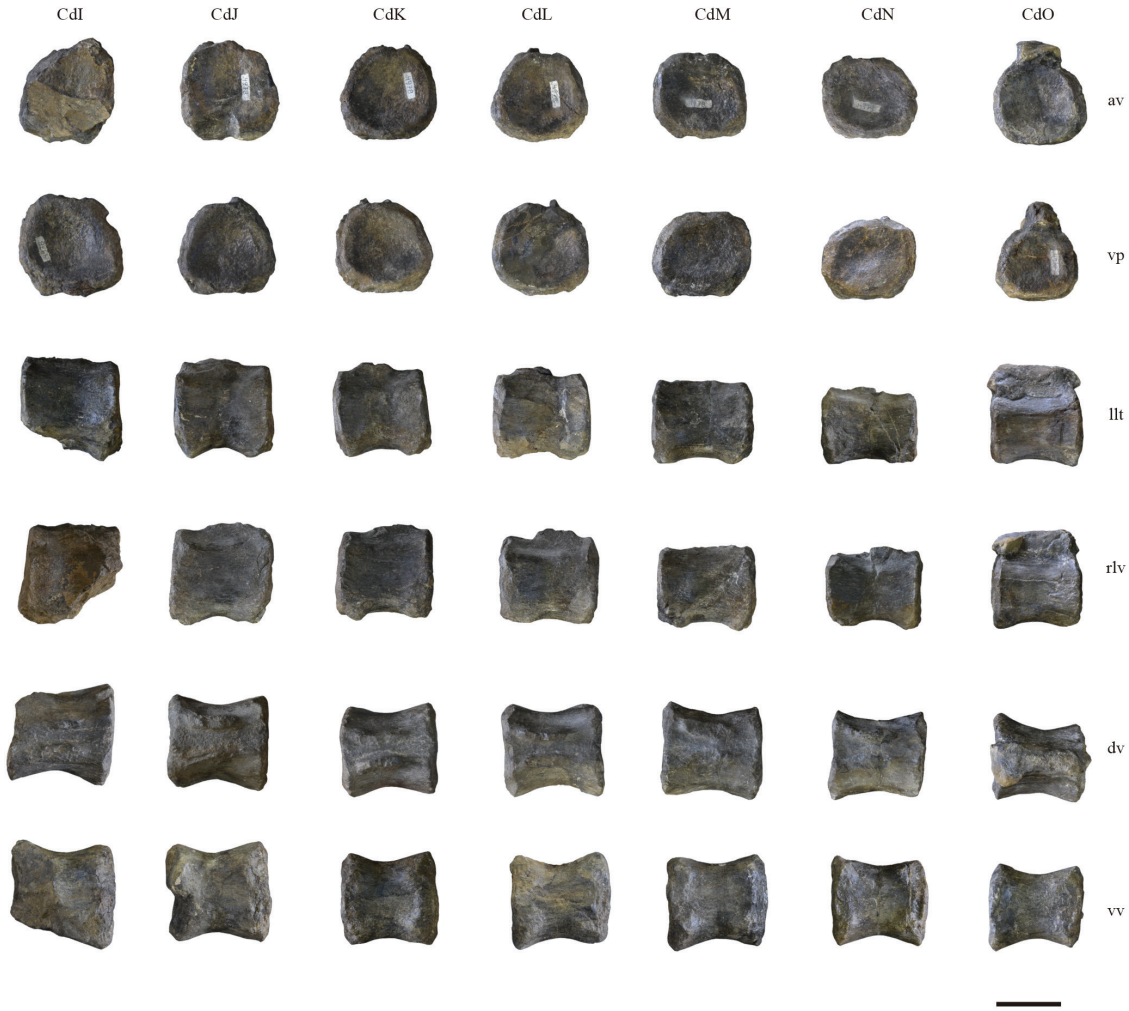

Figure 5.8. Eusauropoda indet., partia caudal series from São Bernardino. Caudal vertebrae from CdI to CdO in anterior (av), posterior (pv), right (rv), left (lv), dorsal (dv) and ventral (vv) views. Scale bar: 10cm.

Discussion: Several partial tails have been described in the Upper Jurassic of Portugal (Lapparent and Zbyszewski, 1957; Mateus, 2005; Yagüe et al., 2006; Mannion et al., 2013; Mocho et al., 2014a), and the tail recovered in São Bernardino, which belong to an individual with an appreciable size, is probably one on the most complete ones. Nevertheless, no vertebra presents a well-preserved neural arch. São Bernardino tail was briefly described and assigned to *Apatosaurus alenquerensis* by Lapparent and Zbyszewski (1957). More recently, Antunes and Mateus (2003) supported this taxonomic attribution, relating this tail with *Lourinhasaurus alenquerensis*. Mateus (2005, p.75) proposed a more careful attribution as cf. *Lourinhasaurus alenquerensis*. This tail does not preserve centra that can be compared directly with *Lourinhasaurus alenquerensis*, since the preserved centra of *Lourinhasaurus* are anterior than the preserved centra of MG 4978. The anterior and middle preserved centra of São Bernardino sauropod are generally dorsoventrally compressed (excluding CdG and CdH) as occur in several basal titanosauriforms (Janensch, 1950; Tidwell et al., 1999, 2001; Upchurch et al., 2004; Canudo et al., 2008; Royo-Torres, 2009) or some eusauropod forms (Upchurch and Martin, 2003).

Middle caudal vertebrae (we consider here as the last anterior caudal vertebrae) with posteriorly projecting caudal ribs, usually reaching the posterior margin of centrum, is considered as a synapomorphy of Titanosauriformes (D'Emic, 2012). The posterior orientation of caudal ribs is a common feature within Titanosauriformes (Mannion et al., 2013) and in some cases they reach and surpass the posterior articulation, as in *Lusotitan* (Mannion et al., 2013), *Sonorasaurus* (Ratkevich, 1998) or *Tastavinsaurus* (Royo-Torres et al., 2009). Some taxa outside Titanosauriformes also project posteriorly the caudal ribs in the last anterior vertebrae such as *Spinophorosaurus* (pers. observ., PM), *Omeisaurus* (Mannion et al., 2013) or *Jobaria* (D'Emic, 2012), but this projection is not so developed as in the referred titanosauriforms. This is the case of MG 4978, the caudal ribs are short and far from the posterior articulations, which distinguish them from the apomorphic condition defined by D'Emic (2012). In sauropods, posteriorly oriented caudal ribs are not present outside Eusauropoda (e.g. Cooper, 1984; Allain and Aquesbi, 2008), so, this feature suggests the proposal of São Bernardino sauropod be a member of Eusauropoda.

In this sauropod, neural arches have a slight anterior displacement, but no so pronounced than in *Lusotitan atalaiensis* and in other titanosauriforms (e.g. Tidwell et al., 2001; Mannion et al., 2013). In conclusion, dorsoventral compressed caudal centra, posteriorly oriented caudal ribs and slight anterior displacement of the neural arch are common features within Eusauropoda and not recorded in basal sauropods (e.g. Cooper, 1984; Allain and Aquesbi, 2008; Bandyopadhyay et al., 2010), suggesting the attribution of the São Bernardino sauropod to Eusauropoda. One particular feature is the presence of a smooth sagittal crest on the ventral face that is just shared by MG 4804 from Salir de Matos (Caldas da Rainha). The validity of this character as a diagnostic feature, that in some cases seems to be affected by the presence of fractures, should be confirmed with new material as well as the relationship between São Bernardino and Salir dos Matos sauropods. The posterior lateral projection on the lateral side of the posterior articulations on the transition between the anterior and the middle caudals are also uncommon and might be a unique feature for this taxon.

5.4.11. Atouguia da Baleia?

Material: Proximal end of a right fibula (MG 30486).

Locality and horizon: MG 30486 is referred with doubt to Atouguia da Baleia (Peniche), Praia da Amoreira-Porto Novo Formation, upper Kimmeridgian-basal Tithonian in age (Manuppella et al., 1999).

Description: A proximal end of a right fibula is preserved (Fig. 5.9a-e). This fibula bears a well-marked tibia scar with a triangular format. On the ventral border of this scar, next to the posterior border of the fibula, there is a pronounced bulge. This scar faces medially, and bears a slight proximal deflection. The anterior trochanter is broken, but it is interpreted that had a crest-like morphology. The lateral trochanter is composed by to crests and an anteroposterior wide concavity. Inside this concavity there are some rugosities slightly displaced posteriorly (i.e. occupy the posterior half of the concavity). The medial face of the fibular shaft is flat.

Discussion: Despite the incompleteness of this fibula, some features can be discussed. The anterior trochanter is not complete but had a crest-like morphology. This morphology is present in derived titanosauriforms such as in *Tastavinsaurus*. D'Emic (2012) suggested that the presence of a crest-like anterior trochanter is a synapomorphy of *Sauroposeidon* + (*Tastavinsaurus* + (Euhelopodidae + (*Chubutisaurus* + Titanosauria))). Nevertheless, in MG 30486 this anterior crest is rudimentary as occur in some non-derived titanosauriforms such as *Lusotitan* (Lapparent and Zbyszewski, 1957; pers. observ., PM), *Turiasaurus* (Royo-Torres et al., 2006) or *Giraffatitan* (Janensch, 1961). Other important feature is the morphology presented by the lateral trochanter. The lateral trochanter shows a wide morphological variability within sauropod (see Royo-Torres, 2009) being difficult to codify in a morphological data matrix. MG 30486 has a wide concave lateral trochanter


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bordered laterally and medially by short proximodistal crests. This morphology is also present in *Turiasaurus riodevensis*, the putative turiasaur found in San Lorenzo (Teruel, Cobos et al., 2011) and in the basal eusauropod *Cetiosaurus oxoniensis* (pers. observ., PM). The presence of lateral trochanters composed by a fossa and bordered by two proximodistal crests is also present in *Suuwassea* (Harris, 2007) and *Rapetosaurus* (Curry Rogers, 2009). Several authors noted for the presence of lateral trochanters composed by two proximodistal crests (e.g. see scoring of Mannion et al., 2013) or the presence of an oval/circular tuberosity associated to a crest, as occurs in *Tastavinsaurus* (Royo-Torres, 2009). The presence of a rudimentary crest-like anterior trochanter and lateral trochanter composed by a wide fossa bordered by two proximodistal crests might be an exclusive for Turiasauria and *Cetiosaurus*, which might relate this specimen to the Eusauropoda clade. *Suuwassea* also presents a wide fossa, but lacks the presence of a rudimentary crest-like lateral trochanter.

Duriatitan Barrett et al., 2010
Duriatitan humerocristatus (Hulke, 1874)
cf. *Duriatitan humerocristatus*

5.4.12. Praia dos Frades

Material: Right humerus (MG 4976), incorrectly identified as a left humerus in the exhibition.

Locality and horizon: Praia dos Frades (Peniche), Praia da Amoreira-Porto Novo Formation, upper Kimmeridgian-to-basal Tithonian in age (Manuppella et al., 1999).

Description: A right humerus lacking the proximal and distal ends (Fig. 5.9f-j). The distal part of the specimen is reconstructed. The deltopectoral crest is rough and laterally directed, with a slight medial deflection. The anterior face of the proximal end lacks any fossa like the fossa that occurs in *Lusotitan* or *Lourinhasaurus* (Mannion et al., 2013; Mocho et al., 2014a), but this could be explained because the incompleteness of the MG 4976 proximal end. In the posterior face of the proximal end, there are a pronounced proximodistal crest behind of the deltopectoral crest, conferring a triradiate outline to the cross-section of the proximal end. The diaphysis is elliptical in cross-section. The distal end is expanded and the anterior face of the most distal preserved part is convex. The humerus exhibits a significant torsion of the extremities. The posterior face of the distal ends bears a slight concavity bordered by two proximal smooth crests that probably would connect with the missing radial and ulnar condyles.

Discussion: MG 4976 is an incomplete humerus with some particular morphological aspects. Lapparent and Zbyszewski (1957) referred the discovery of a right humerus in Praia de Frades, which probably corresponds to MG 4976. This humerus was firstly related to *Apatosaurus alenquerensis* (Lapparent and Zbyszewski, 1957) due the presence of some shared features such as the narrowness of the shaft and the position of the deltopectoral crest. Antunes and Mateus (2003) attributed this humerus to *Lourinhasaurus alenquerensis* and Mateus (2005) proposed an uncertain identification to ?*Lourinhasaurus alenquerensis*. Besides the differences in size, that might suggest different ontogenetic stages, MG 4978 bears some important differences

Figure 5.9. Eusauropoda indet., proximal end of a right fibula (MG 30486) from ?Atouguia da Baleia (Peniche) in lateral (a), medial (b), anterior (c), posterior (d) and proximal (e) views. Cf. Duriatitan humerocristatus, partial right humerus (MG 4976) from Praia dos Frades (Peniche) in anterior (f), posterior (g), lateral (h), medial (i) and proximal (j) views (the proximal end of MG 4976 is not complete). Sauropoda indet., distal end of humerus (MG 30484) from ?Alenquer in posterior (k) view. Titanosauriformes indet., a proximal end of left femur (MG 4986) from Praia da Areia Branca (Lourinhã) in proximal (l), posterior (m), anterior (n), lateral (o) and medial (p) views. Scale bar: 10cm.

when compared with the humeri of *Lourinhasaurus* and other Iberian Upper Jurassic taxa such as *Lusotitan*, *Aragosaurus*, *Zby*, *Turiasaurus*, *Losillasaurus* and *Galveosaurus* (Sanz et al., 1987; Casanovas et al., 2011; Royo-Torres et al., 2006, 2014; Barco, 2009; Mannion et al., 2013; Mateus et al., 2014; Mocho et al., 2014a).

The deltopectoral crest in this humerus is dorsoventrally restricted as occur in Turiasauria (Royo-Torres et al., 2006; Mateus et al., 2014) and Brachiosauridae (Janensch, 1961; Tidwell et al., 1999; Mannion et al., 2013), but not in *Lourinhasaurus* (Mocho et al., 2014a). On the other hand, the distal end of the humerus present an appreciable torsion respect to the proximal end, as occur in other sauropods (e.g. Salgado and Bonaparte, 1991; Harris, 2007), but absent in *Lourinhasaurus*, *Galveosaurus*, *Zby*, *Turiasaurus*, *Losillasaurus* and *Aragosaurus* (Casanovas et al., 2001; Royo-Torres et al., 2006, 2014; Barco, 2009; Mateus et al., 2014; Mocho et al., 2014a). Dorsoventrally restricted deltopectoral crests seems to be restricted to some eusauropod groups (Turiasauria and Brachiosauridae), suggesting the relationships of MG 4976 with the Eusauropoda clade.

Other feature that seems to be exclusive of this humerus in the context of the Iberian Upper Jurassic sauropods is the presence of a proximodistal crest on the posterior face of the proximal end, behind the deltopectoral crest. This feature is also described as an autapomorphy of *Duriatitan humerocristatus* found in the British Upper Jurassic sediments of the Clay Formation, lower Kimmeridgian in age (NHMUK 44635, Barrett et al., 2010). Based on its slenderness, some authors considered that this humerus might represent a brachiosaurid (e.g. McIntosh, 1990a, b; Upchurch and Martin, 2003; Upchurch et al., 2004). Barrett et al. (2010) and Mannion et al. (2013) retained a more cautiously attribution considering it as a basal titanosauriform. Mannion et al. (2013) noted for the slenderness of the humerus of the non-neosauropod *Lapparentosaurus* from the Middle Jurassic of Madagascar. Although the bad state of preservation, these authors considered that the deltopectoral crest might presents a slight medial orientation that could relate this humerus to Titanosauriformes. Nevertheless, slight medial displacement is also observed outside Titanosauriformes such in *Cetiosaurus* (Upchurch and Martin, 2003). When compared with *Duriatitan*, MG 4976 also present a similar deltopectoral crest orientation: anteriorly projected, but occupying a slight medial displacement. If we accept the acute crest on the posterior face of proximal end as an exclusive feature for *Duriatitan*, MG 4976 should be related to this taxon of the British Upper Jurassic. However, at the moment, and taking into account the incompleteness of MG 4976 and NHMUK 44635 specimens, we consider the humerus from Praia de Frades as cf. *Duriatitan humerocristatus*.

Neosauropoda Bonaparte, 1986
Neosauropoda indet.

5.4.13. Castanheira

Material: Middle or posterior dorsal vertebra (MG 4799).

Locality and horizon: Castanheira (Vila Franca de Xira), Abadia Formation, lower-to middle (?) Kimmeridgian (Leinfelder and Wilson, 1989; Kullberg et al., 2006).

Description: Partial centrum of a middle or posterior dorsal vertebra, being preserved only the right side (Fig. 5.10). The centrum is opisthocoelous, that is bears a concave posterior articular face and a convex anterior one. The ventral margin of the pleurocoel is preserved, and its ventral surface slopes ventromedially, suggesting that the pleurocoel is deep.

Discussion: MG 4799 was firstly referred as a metatarsal V of *Apatosaurus alenquerensis* (Lapparent and Zbyszewski, 1957). In a recent revision of this specimen, Mannion et al. (2013) considered it as a procoelous caudal vertebra. Nevertheless, herein this specimen is reinterpreted

as partial dorsal vertebrae. Deep pleurocoels on dorsal vertebrae are common in neosauropods such as diplodocoids (excluding Dicraeosauridae, *sensu* Salgado et al., 1997) and basal macronarians (Wedel, 2003; Upchurch et al., 2004), and was considered as a synapomorphy of *Omeisaurus*+Neosauropoda by Wilson and Sereno (1998). This vertebrae could be distinguished from those of the turiasaurs, because in the members of this group (*Turiasaurus* and *Losillasaurus*), the pleurocoels are only medially deeper as also occurs in most basal eusauropods such as *Jobaria* (Sereno et al., 1999), *Cetiosaurus oxoniensis* (Upchurch and Martin, 2003), *Cetiosauriscus* (pers. observ., PM), *Patagosaurus* (Bonaparte, 1986) or *Spinophorosaurus* (Remes et al., 2009). Assuming the absence of mamenchisaurids outside Asia during the Upper Jurassic (Carballido and Sander, 2014), is acceptable to consider that this dorsal vertebra represent to an indeterminate neosauropod.

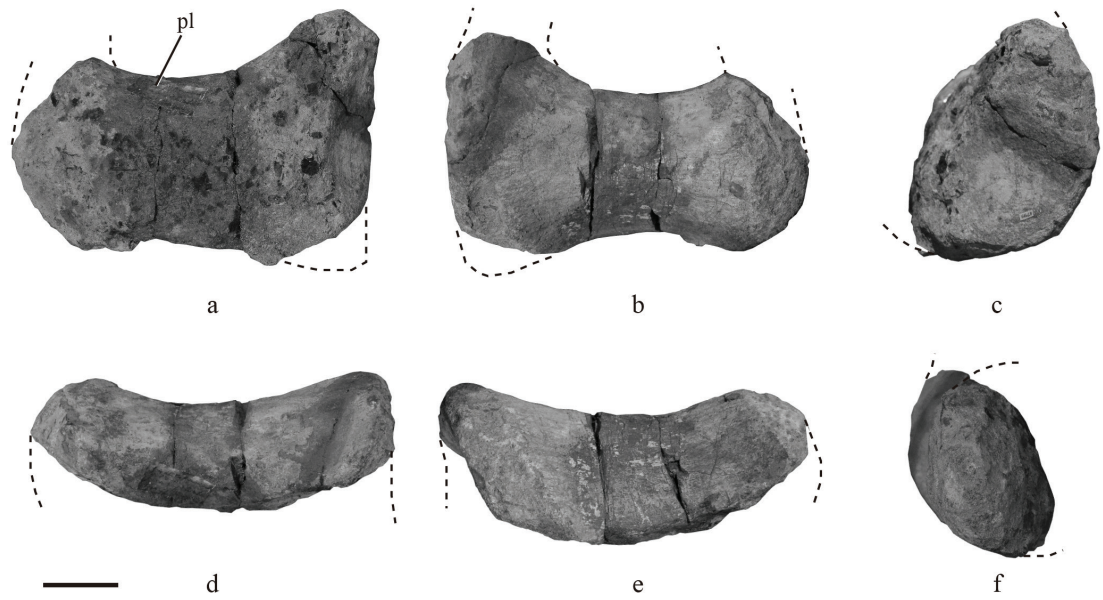

Figure 5.10. Neosauropoda indet., partial dorsal centrum (MG 4799) from Castanheira (Vila Franca de Xira) in left (a), right (b), posterior (c), dorsal (d), ventral (e) and anterior (f) views. Scale bar: 5cm.

Diplodocoidea Marsh, 1884
Flagellicaudata Harris and Dodson, 2004
Diplodocidae Marsh, 1884 (*sensu* Upchurch 1995)
Diplodocinae Janensch 1929
Diplodocinae indet.

5.4.14. São Gregório da Fanadia

Material: Three incomplete middle-to-posterior caudal vertebrae (MG 4819, 4821, 4826).

Locality and horizon: Porto de Barros, 150m NW of São Gregório da Fanadia (Caldas da Rainha), Bombarral Formation, Tithonian in age (Manuppella et al., 1999, 2000; Kullberg et al., 2006; Azerêdo et al., 2010).

Description: In the collections of the Museu Geológico there are three incomplete centra of caudal vertebrae that were previously related to *Megalosaurus* (Lapparent and Zbyszewski, 1957), but are considered here as representing a member of Sauropoda (Fig. 5.11). Taking into account the

presence of the same general morphology they will be described together. There are two posterior articular faces (MG 4819 and MG 4826, Fig. 5.11a-e and Fig. 5.11k-o, respectively) and one anterior one (MG 4821, Fig. 5.11f-j). Lapparent and Zbyszewski (1957) referred the presence of one caudal vertebra into two pieces and MG 4819 and MG 4821 might pertain to the same vertebra, however, they do not fit together. If these two fragments are a unique vertebra, the ratio of centrum length to centrum height for this centrum is higher than 2.0. The preserved anterior articular face is flat as well as one of the posterior ones. The articular face of MG 4826 is slightly concave and probably represents the most posterior centrum of this set. The articular faces are wider next to the ventral border. They have a sub-quadrangular cross-section with marked ventrolateral crests. These ventrolateral crests delimit a transversely concave ventral face. The lateral face bears a smooth fossa. Besides the weak state of preservation, the anterior and posterior articular facets for chevrons are preserved. In lateral view, they present an appreciable ventral development. In MG 4821, the neural arch almost reach the anterior articulation. On the other hand, in MG 4819 and MG 4826, the neural arch is not so near to the posterior articulation. In MG 4826, the neural arch is not fused to the centrum, suggesting that it does not belong to a mature individual.

Discussion: One vertebra in two pieces was identified by Lapparent and Zbyszewski (1957), but in the collections there are three fragments of at least two caudal vertebrae (the union between MG 4819 and MG 4821 is not confirmed). MG 4826 is figured by Lapparent and Zbyszewski (1957, pl. XXV, fig. 86). These vertebrae were considered caudal vertebrae of *Megalosaurus pombali* (Lapparent and Zbyszewski, 1957), a taxon considered as *nomina dubia* by Antunes and Mateus (2003). Mateus (2005) related them to an indeterminate theropod.

In the MG 4821 label was found de following note: "*Barosaurus* at *Diplodocus*" from McIntosh dated of 15/10/1973. Despite of the fragmentary state of these three middle/posterior caudal centra, they have an important combination of features. The presence of a well-developed concave ventral face on anterior, middle and posterior caudal vertebrae bordered by well-marked lateroventral crests were acquired at least two time along the evolutionary history of sauropods: in diplodocines (Osborn, 1904; McIntosh, 2005; Remes, 2006; Whitlock, 2011) and in some titanosaurs such as saltasaurids (e.g. Powell, 1992; Wilson, 2002; Upchurch et al., 2004; Gomani, 2005). The presence of a longitudinal ventral hollow on anterior and middle caudal vertebrae was considered as synapomorphy of Diplodocinae (e.g. Wilson, 2002; Carballido et al., 2011) as well as for Titanosauria (e.g. Wilson, 2002; D'Emic, 2012). Nevertheless, this feature present a uncertain phylogenetic distribution within titanosauria, or even within Titanosauriformes (depending the phylogenetic approach) being present in the some Chinese somphospondylians such as *Daxiatitan*, *Huanghetitan liujiaxiaensis* and *H. ruyangensis* (placed within Titanosauria *sensu* Mannion et al., 2013).

The presence of a quadrangular cross-section of the centrum was also considered as a synapomorphy of Diplodocinae (Wilson, 2002; Carballido et al., 2011; but Whitlock, 2011 restricted this feature only for anterior caudal vertebrae: character #136) and allows placing these vertebrae within this clade. This condition differs from the more cylindrical middle caudal vertebrae of titanosaurs (e.g. Powell, 1992; Gomani, 2005; D'Emic, 2012). The flat articulations also distinguish these caudal vertebrae from the procoelous middle caudal vertebrae of lithostrotian titanosaurs (e.g. Powell, 1992; Salgado et al., 1997; Sanz et al., 1999; Gomani, 2005). The general morphology of these vertebrae is indistinguishable from that of the middle and posterior caudal vertebrae of the diplodocines *Diplodocus*, *Barosaurus* and *Tornieria*. The presence of fossae in the lateral face of middle caudal vertebra are only recorded in the Morisson and Tendaguru diplodocines (Osborn, 1904; McIntosh, 2005; Lucas et al., 2006; Remes, 2006) and in some cases they are perforated by foramina as occur in *Diplodocus* (e.g. Osborn, 1904). The presence of lateral fossae, transversely concave ventral surfaces bordered by well-developed lateroventral crests and a quadrangular cross-section are the criteria to relate these vertebrae to an indeterminate diplodocine.

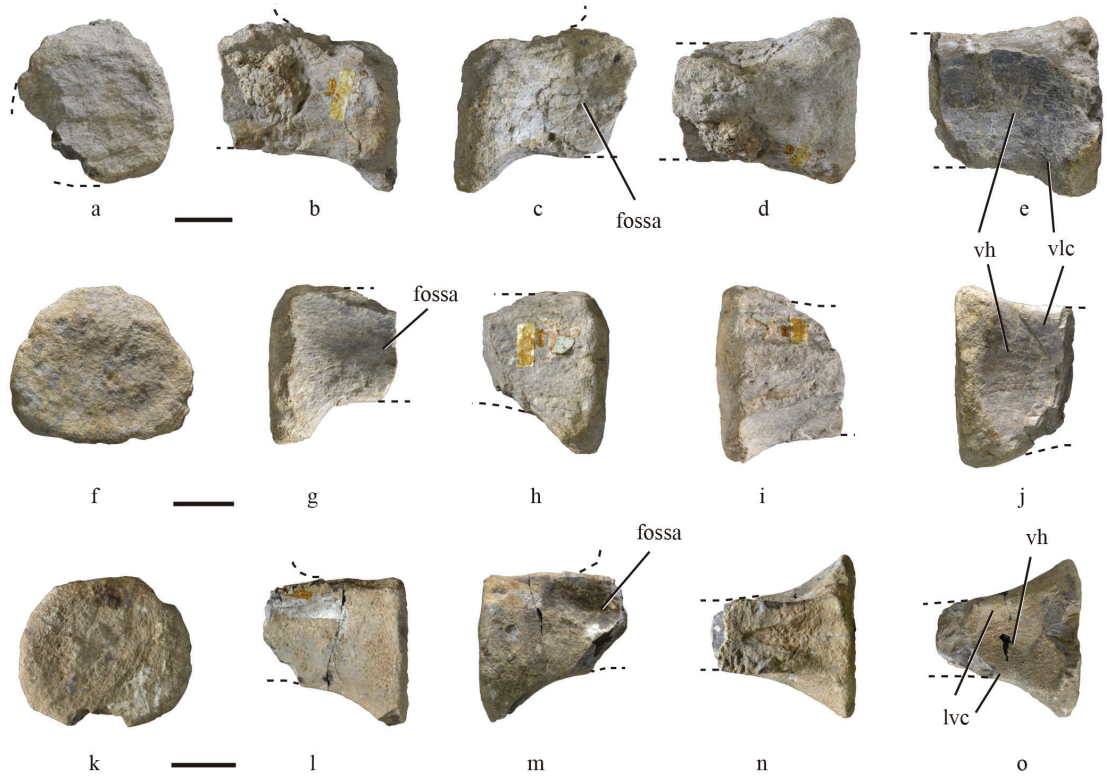

Figure 5.11. Diplodocinae indet., middle and posterior caudal vertebrae (MG 4819, 4821, 4826) from São Gregório da Fanadia (Caldas da Rainha). MG 4819 in posterior (a), left (b), right (c), dorsal (d) and ventral (e) views. MG 4821 in anterior (f), left (g), right (h), dorsal (i) and ventral (j) views. MG 4826 in posterior (k), left (l), right (m), dorsal (n) and ventral (o) views. Scale bar: 5cm.

5.4.15. Porto Novo II

Material: Six associated fragments including three incomplete middle/posterior caudal centra (MG 25197.4-6), two dorsal rib fragments (MG 25197.1 and MG 25197.3), and an indeterminate element (MG 25197.2).

Locality and horizon: Porto Novo, Maceira (Torres Vedras), Praia da Amoreira-Porto Novo Formation, upper Kimmeridgian-basal Tithonian in age (Manuppella et al., 1999).

Description: Three fragments of incomplete middle caudal vertebrae from which not too much information is possible to obtain, and so, they are not figured. The preserved articular faces (anterior or posterior) are flat to concave. The articular facets for the chevrons are not preserved. The ventral face is transversely concave and bordered by well-developed ventrolateral crests.

Discussion: The presence of transversely concave ventral surfaces bordered by well-developed lateroventral crests and a quadrangular cross-section are used to relate this remains with the Diplodocinae clade (see discussion in section for the vertebrae found in São Gregório da Fanadia, MG 4819, 4821 and 4826).

Macronaria Wilson and Sereno, 1998
Titanosauriformes Salgado et al., 1997
Titanosauriformes indet.

5.4.16. Praia de Areia Branca

Material: Left incomplete femur (MG 4986).

Locality and horizon: Praia de Areia Branca, Bombarral Formation dated to Tithonian (Manuppella et al., 1999).

Description: MG 4986 is a left femur (Fig. 5.9l-p) of large size. It corresponds to one of larger femurs found in the Portuguese Upper Jurassic, but only the proximal end is preserved. The femur has a straight shaft in lateral and anterior views. The femoral head is dorsomedially projected, being thicker anteroposteriorly than the region of the greater trochanter. The anterior face of the femoral head is eroded as the posterior face of the proximal end of the femur. The *linea intermuscularis cranialis* on the anterior face of the femoral shaft is absent. The proximal one-third of the femur is deflected medially, resulting in a marked lateral bulge on the lateral face of the femur. This lateral bulge is thicker anteroposteriorly in the point of the deflection. On the posterior face, there is an incipient trochanteric shelf below the greater trochanter region. The shaft is compressed anteroposteriorly (ratio transverse/anteroposterior width of the shaft is 2,76). The region of the fourth trochanter is eroded.

Discussion: A proximal portion of a large femur from Praia de Areia Branca was reported by Lapparent and Zbyszewski (1957) and was related to *Brachiosaurus atalaiensis*, now *Lusotitan atalaiensis* (Antunes and Mateus, 2003). Antunes and Mateus (2003) retained the assignation for the Areia Branca femur to *Lusotitan atalaiensis*. The femur present a lateral bulge that has been referred as a synapomorphy of Titanosauriformes (e.g. Salgado et al., 1997; Wilson, 2002; Upchurch et al., 2004; D'Emic, 2012) or a more inclusive group inside Macronaria (Carballido et al., 2011; Carballido and Sander, 2014). Some derived diplodocids also acquired a lateral bulge (e.g. Hatcher, 1901; Lull, 1919; McIntosh, 2005). The diaphysis has a marked anteroposterior compression as noted Mannion et al. (2013), greater than that of any other Iberian Upper Jurassic sauropods such as *Lourinhasaurus alenquerensis* (Mocho et al., 2014), *Turiasaurus riodevensis* (Royo-Torres et al., 2006), the San Lorenzo turiasaur (Cobos et al., 2011) and *Aragosaurus ischiaticus* (Sanz et al., 1987; Royo-Torres et al., 2014). The value presented by this femur for the ratio transverse/anteroposterior width fist in the range that seems to be synapomorphic of Titanosauriformes (Wilson, 2002; Upchurch et al., 2004; see values presented by Mannion et al., 2013).

Other feature generally present in Titanosauriformes is the trochanteric shelf on the posterior surface of the proximal end. This structure was suggested as a synapomorphy of Saltasaurinae (Otero, 2010), but D'Emic (2012) suggested that is diagnostic for a more inclusive group including saltasaurins and *Alamosaurus*. Nevertheless, this trochanteric shelf seems to be more widely distributed in titanosauriforms, being present in other titanosaurs such as *Jainosaurus* (Wilson et al., 2011), *Lirainosaurus* (Díez-Díaz et al., 2013), *Rapetosaurus* (Curry Rogers, 2009), *Ampelosaurus* (Le Louff, 2005) or in basal titanosauriforms such as *Tastavinsaurus* (Royo-Torres, 2009) or *Giraffatitan* (Janensch, 1961). In the case of MG 4986, the trochanteric shelf is not so well-developed as in *Giraffatitan* or *Tastavinsaurus* (pers. observ., PM). The presence of a pronounced bulge, a trochanteric shelf and an anteroposterior compressed femoral shaft allow us to conclude that this femur could be attribute to an indeterminate titanosauriform.

5.4.17. Alenquer?

Material: Pubic peduncle from an ilium (MG 30485).

Locality and horizon: This bone is on a box with the reference of Moinho Carmo (Alenquer), locality of *Lourinhasaurus alenquerensis* lectotype. Nevertheless, this reference seems to be

scratched. From Moinho Carmo, only one individual was recognized in the field and collections (Lapparent and Zbyszewski, 1957; Mocho et al., 2014a) besides the presence of some elements that was clearly mixed with the lectotype of *Lourinhasaurus alenquerensis* due the different state of preservation (part of this material were moved to different facilities). Furthermore, the morphology of this pubic peduncle is particular distinct from *Lourinhasaurus* (see below).

Description: The pubic peduncle of an ilium is preserved in the collections of the Museu Geológico (Fig. 5.12). This peduncle is transversely elongated and in distal view, it bears an arched profile with the convexity facing anteriorly. The distal surface is rough. The anterior and posterior face of the peduncle is convex and concave transversely, respectively.

Discussion: Transversely elongated pubic peduncle on the ilium is considered as a synapomorphy of Titanosauriformes clade (iliac pubic peduncle more than 1.5 times wider than long anteroposteriorly, D'Emic, 2012) and present in MG 30485. MG 30485 differ from the morphology presented by *Lourinhasaurus* with a subtriangular outline, common in other non-titanosauriform sauropods such as *Camarasaurus* (Osborn and Mook, 1921; Ostrom and McIntosh, 1966), *Haplocanthosaurus* (Hatcher, 1903) or *Diplodocus* (Hatcher, 1901). For no other Iberian Upper Jurassic sauropod have been described a transversely elongated iliac pubic peduncle (Casanovas et al., 2011; Royo-Torres et al., 2006, 2014; Barco, 2009; Mannion et al., 2012, 2013; Mateus et al., 2014).

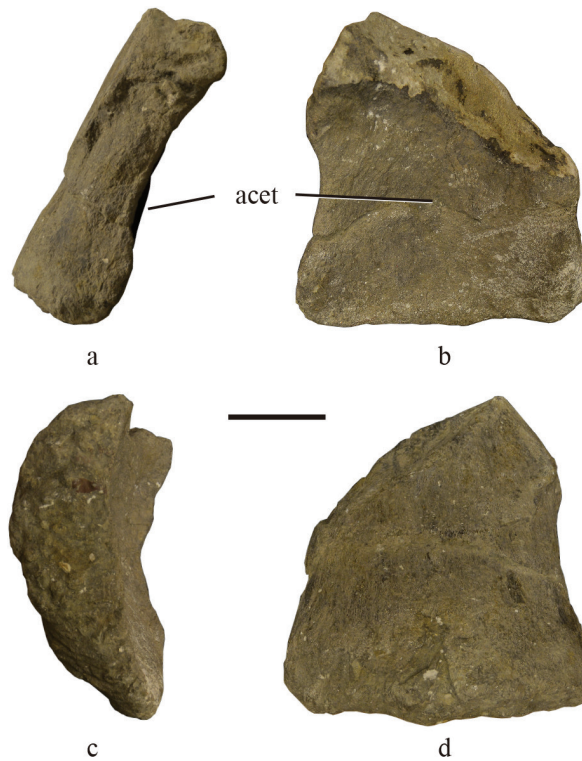

Figure 5.12. Titanosauriformes indet., iliac peduncle (MG 30485) from ?Alenquer in lateral or medial (1), posterior (2), ventral (3) and anterior (4) views. Scale bar: 10cm.

Lusotitan Antunes and Mateus, 2003
Lusotitan atalaiensis (Lapparent and Zbyszewski, 1957)
cf. *Lusotitan atalaiensis*

5.4.18. Maceira

Material: Middle caudal vertebra (MG 8804).

Locality and horizon: In the present label it is referred that this vertebra was found in "*Corte da Foz Velha de Maceira para Cambelas*", possible from sediments of Freixial Formation, Tithonian in age (Pereda-Suberbiola et al., 2005; Kullberg et al., 2006).

Description: A middle caudal vertebra is preserved lacking the neural arch (Fig. 5.3g.I-g.VI). The dorsal surface of the centrum is eroded but the neural arch seems to be anteriorly displaced. The centrum is dorsoventrally compressed and both articulations are concave. The anterior articulation becomes wider ventrally. The lateral face of the centrum is convex and lacks evidence of longitudinal crests. The ventral face is convex-to-flat and bears in the anterior border undeveloped and semi-elliptical articulations for the chevrons. Posteriorly to the anterior articulations, there are two anteroposteriorly elongated fossae as occur in the middle caudal vertebrae of *Lusotitan* lectotype (pers. observ., PM).

Discussion: This bad preserved middle caudal vertebra bears some features that allow us to obtain a more precise identification. MG 8804 was firstly related to *Brachiosaurus atalaiensis* (Lapparent and Zbyszewski, 1957, pl. XXVI, fig. 95) and to *Lusotitan atalaiensis* (Antunes and Mateus, 2003). This centrum is dorsoventrally compressed as in *Lusotitan atalaiensis*, several other basal titanosauriforms (Janensch, 1950; Tidwell et al., 1999, 2001; Upchurch et al., 2004; Canudo et al., 2008; Royo-Torres, 2009) and *Galveosaurus* (Barco, 2009). Nevertheless, as it was referred before, *Cetiosaurus oxoniensis* also present middle caudal centra with an appreciable dorsoventral compression. This centrum also present a marked anterior displacement of the neural arch as in Titanosauriformes (Salgado et al., 1997; D'Emic, 2012; Mannion et al., 2013) and as in the non-neosauropod eusauropod *Cetiosaurus oxoniensis* (Upchurch and Martin, 2003). This combination of features (anterior displacement of the neural arch on middle caudals and dorsoventral compressed caudal centra) could not be used to place this vertebra within Titanosauriformes due the presence of convergence outside this clade, more precisely with *Cetiosaurus*. Other particular feature observed in MG 8804 is the presence of two circular depressions behind the anterior articulations for the chevrons. These depressions are also observed in *Lusotitan atalaiensis* lectotype, and might represent an autapomorphy. According to this feature, this centrum is tentatively referred to *Lusotitan atalaiensis*. Excluding this feature as diagnostic of *Lusotitan*, MG 8804 should be considered as an indeterminate eusauropod by the presence of the following combination of characters: anterior displaced neural arch on middle caudal vertebra and dorsoventral compressed centra.

5.4.19. Other material

In the Museu Geológico several other specimens are also found such as the lectotype of *Lourinhasaurus alenquerensis* and *Lusotitan atalaiensis* described in detail by Mocho et al. (2014a) and Mannion et al. (2013), respectively (see numbers in S.2). Nevertheless, other fragmentary specimens related to Sauropoda clade were also identified in the collections.

Three fragments (MG 25254.2-4) are associated and were found in a locality between Foz Velha da Maceira and Cambelas (Torres Vedras), one middle/posterior caudal vertebra (MG 25254.2) and thee indeterminate fragments. MG 25254.2 is a middle or posterior caudal vertebra with a cylindrical form. The preserved articulation is concave. The ventral face is convex lacking ventrolateral or sagittal crests. There are rudimentary articulations for the chevrons. Between these articulations de ventral surface is slightly concave. The vertebra is related to an indeterminate sauropod. The indeterminate fragments should not be related to this clade.

Three heart-shaped tooth are also found in the collections from Fervença (MG 277), São Martinho do Porto (MG 4832) and Ourém (MG 16). Those have been referred in several studies (Sauvage, 1897-98; Lapparent and Zbyszewski, 1957; Royo-Torres et al., 2006, 2009; Mocho et al., 2012) and they were recently referred with doubt to Turiasauria clade (Mocho et al., 2012, in press). Another tooth with a cone-chisel morphology is also present in the collections (MG 125, Sauvage, 1897-98; Lapparent and Zbyszewski, 1957). This cone-chisel morphology is common in Titanosauriformes teeth (see Calvo, 1994). A detailed description and discussion of this tooth and unpublished cone-chisel teeth of the Portuguese Upper Jurassic is in progress. Finally, two teeth fragments (MG 8771) were found in association to material attribute to *Omasaurus lenieri* and found in Porto das Barcas (Lourinhã), where outcrops the sediments of the Sobral Fm., upper Kimmeridgian-basal Tithonian in age. These teeth present a wrinkled texture that allow us to related them to an indeterminate sauropod (e.g. Carballido and Pol, 2010).

MG 8803 is fragment from a tibial distal end, most precisely part of the articular surface for the ascending process. This specimen was collected in Serra da Vila (Torres Vedras, locality referred on the figure 1 of Lapparent and Zbyszewski, 1957) and probably from the sediments of the Sobral Formation, upper Kimmeridgian-basal Tithonian in age. MG 8792 are two dorsal rib fragments with an appreciable size, probably related to an indeterminate sauropod and they were found in Atalaia (Lourinhã) from the sediments of Sobral Fm., upper Kimmeridgian-basal Tithonian in age. An isolated middle caudal vertebra (MG 8802) found in the collections with unknown locality is related to an indeterminate sauropod. Some dorsal rib fragments (MG 30480), including a proximal end, were found in Ribamar (Lourinhã) where outcrops the Praia de Amoreira-Porto Novo Fm. (Manuppella et al., 1999). A partial caudal neural spine (MG 30481) and a partial dorsal centrum (MG 30482) are associated in the collections of the Museu Geológico and are referred with doubt to the Atalaia locality (Lourinhã, Sobral Fm.). The association of these two bones on the field is not confirmed. The dorsal centrum bears deep pleurocoels, suggesting that it might represent a neosauropod form (see discussion for MG 4799). The anterior caudal neural spine do not bears diagnostic features and is considered to pertain an indeterminate sauropod. A humeral partial distal end (MG 30484, Fig. 5.9k) with a transversely flat distal articulation of an indeterminate sauropod is referred with doubt to Alenquer locality. Finally, a set of bad preserved anterior and middle caudal vertebrae with indeterminate fragments associated (MG 30390) were found in Porto das Barcas (Lourinhã, Sobral Formation) and they were offered to the Museu Geológico by Carlos Abreu Baptista. One of these caudal vertebrae bears a slight procoelous condition. Procoelous anterior caudal vertebrae are only present in eusauropods such as mamenchisaurids (e.g. Ouyang and Ye, 2002), turiasaurs (Casanovas et al., 2001; Royo-Torres et al., 2009), diplodocoids (e.g. Osborn, 1904; Hatcher, 1901; Lull, 1919) and titanosaurs (e.g. Powell, 1992; Salgado et al., 1997; Coria et al., 2013). Carballido and Sander (2014) considered that titanosaurs bears a more pronounced procoelous condition on anterior caudal vertebrae (also observed in *Mamenchisaurus* and *Bellusaurus*), differing from the slight procoelous condition of MG 30390. The presence of a longitudinal ventral hollow on anterior and middle caudal vertebrae was considered as a synapomorphy of Diplodocinae (e.g. Wilson, 2002; Carballido et al., 2011) and Titanosauria (e.g. Wilson, 2002; D'Emic, 2012) and are absent in MG 3039.

5.5. MUSEU GEOLÓGICO COLLECTIONS IN THE CONTEXT OF THE SAUROPOD FAUNAS OF THE IBERIAN UPPER JURASSIC.

The Museu Geológico sauropod collections represent nowadays one of the most important sauropod collections in Iberian Peninsula with two lectotypes (*Lourinhasaurus alenquerensis* and *Lusotitan atalaiensis*) and several other specimens related to this group. Although the historical significance of these collections, with some of the first referred, described and figured sauropod specimens of the Portuguese Mesozoic (Sauvage, 1897-98; Lapparent and Zbyszewski, 1957);

they were also important for the understand of the evolutionary history of the sauropod faunas present in the Upper Jurassic of the Lusitanian Basin (Lapparent and Zbyszewski, 1957; Dantas, 1990; McIntosh, 1990a, b; Dantas et al., 1992, 1998; Wilson and Sereno, 1998; Bonaparte and Mateus, 1999; Rauhut, 2000; Antunes and Mateus, 2003; Upchurch et al., 2004; Mateus, 2005). More recently, Portuguese Upper Jurassic sauropods start to be revised and new phylogenetic approaches are being proposed (Mannion et al., 2012, 2013; Mocho et al., 2014a). Furthermore, new specimens are being discovery and described (Yagüe et al., 2006; Mateus, 2005; Mocho et al., 2012, 2013b, 2014b; Mateus et al., 2014), urging the necessity to revise the systematic approach of other classical specimens that were found in the last part of the 19th century and in the first half of the 20th century as noted Dantas (1990). Up today, no detailed work was published for the most part of the classical material housed in the Museu Geológico, with some intents, with works of an inventory nature, proposed by Antunes and Mateus (2003) and Mateus (2005). Excluding MG 8804, previous systematic approaches, which relate these specimens to *Lourinhasaurus* and *Lusotitan* genera, are not supported or impossible to test.

This study propose a new systematic approach for the available sauropod remains present in these collections. Several groups are represented, including basal eusauropods, diplodocines, camarasaurids and basal titanosauriforms. Several specimens are considered as Sauropoda indet. such as MG 4811 (Albergaria dos Doze, Pombal); MG 8809 (Atalaia, Lourinhã); MG 8805 (Porto das Barcas, Lourinhã), MG 4802 (Alto da Vela, Torres Vedras), MG 4800 (Porto Novo, Torres Vedras) and MG 8799 (Praia de Almoinhas?). This material do not bears important diagnostic features in order to provide a more complete systematic evaluation. According to the available information about the Upper Jurassic sauropod faunas (e.g. Wilson, 2002; Upchurch et al., 2004; D'Emic, 2012; Mannion et al., 2013), they probably represent members within Eusauropod clade, being unknown, up to the moment, Upper Jurassic basal sauropods non-eusauropod forms (e.g. Upchurch et al., 2004; Remes et al., 2009).

Several specimens were related to Eusauropoda, and the major part is uninformative for a more precise systematic contest such as MG 8800 (Porto das Barcas, Lourinhã), MG 4804 (Salir de Matos, Caldas da Rainha) and MG 4978 (São Bernardino, Peniche). In particularly, São Bernardino tail bears two uncommon features, the presence of a smooth longitudinal crest on the ventral face, and lateral projections in the point where the longitudinal lateral crests and the posterior articulation meet each other, in the last anterior caudal vertebrae. These uncommon features may represent two diagnostic features for an unknown eusauropod of the Portuguese Upper Jurassic, but, according the incompleteness of the present specimen, we decided to attribute it to an indeterminate eusauropod. The longitudinal ventral smooth crest might relate MG 4804 to the São Bernardino sauropod.

MG 4976 is left humerus and shares the presence of an posterior and acute proximodistal crest on the its proximal end with *Duriatitan humerocristatus*, being considered as cf. *Duriatitan humerocristatus* up to found more complete specimens. The presence of proximodistal restricted deltopectoral crest allow us to relate this taxon to Eusauropoda clade. *Duriatitan* is an Upper Jurassic sauropod of the British Upper Jurassic. MG 4976 and the holotype of *Duriatitan* (NHMUK 44635) suggest some putative affinities between the Portuguese and British Upper Jurassic sauropod faunas. Although, the Portuguese Upper Jurassic sauropods have been classical related with Morrison Formation sauropods (e.g. Lapparent and Zbyszewski, 1957; McIntosh, 1990a, b; Mateus, 2006; Ortega et al., 2009, 2013), the presence of some affinities to European forms have been confirmed with the presence of turiasaurian remains in the Lusitanian Basin (Royo-Torres et al., 2006, 2009, 2014; Mateus, 2009; Ortega et al., 2010; Mocho et al., 2012, in press; Royo-Torres and Upchurch, 2012; Mateus et al., 2014). This group was firstly found in the Spanish Upper Jurassic-Lower Cretaceous of the Villar del Arzobispo Fm. (Royo-Torres et al., 2006) and represented by two established taxa: *Turiasaurus riodevensis* (Royo-Torres et al.,

2006) and *Losillasaurus giganteus* (Casanovas et al., 2001). This group seems to be restricted to the European territory during the Upper Jurassic (e.g. Royo-Torres et al., 2006, 2009, 2014; Royo-Torres and Upchurch, 2012; Mocho et al., in press). MG 16, 277, 4832 are three teeth from Museu Geológico collections and tentatively related to Turiasauria (Royo-Torres et al., 2006, 2009; Mocho et al., 2012, in press; Royo-Torres and Upchurch, 2012).

Some specimens are related to Neosauropoda. The re-evaluation of MG 4799 (Castanheira, Alenquer) allow us to relate it to an indeterminate neosauropod due the presence of deep pleurocoels. At the moment, three neosauropod taxa have been recognized for the Portuguese Upper Jurassic, all of them bear ventrally deep pleurocoels (Mannion et al., 2012, 2013; Mocho et al., 2014a). The reevaluation of three caudal centra referred to *Megalosaurus pombali* of São Gregório da Fanadia (Caldas da Rainha, MG 4819, 4821, 4826) and caudal centra fragments from Porto Novo (Torres Vedras, MG 25197.4-6) with the presence of lateral fossae, quadrangular cross-section and transversely concave ventral face bordered by ventrolateral crests allow us to relate this material to the diplodocid clade, Diplodocinae. Diplodocidae clade is recorded in the Lusitanian Basin Upper Jurassic by the presence of *Dinheirosaurus* (Dantas et al., 1992; Bonaparte and Mateus, 1999; Mannion et al., 2012); Moita dos Ferreiros diplodocid (Mateus, 2005; Mannion et al., 2012), and the three new diplodocid specimens with diplodocine affinities (SHN (JJS) 177, 178, 179, Mocho et al., 2014b).

Finally, MG 4986 (Praia da Areia Branca) is related to an indeterminate titanosauriform by the presence of the following character combination: the presence of a lateral bulge and anteroposteriorly compressed shaft. MG 8804 (Maceira, Torres Vedras) is related to *Lusotitan atalaiensis* with doubt, by the presence of circular smooth fossae in the ventral face of the middle caudal centra, a putative autapomorphy of *Lusotitan atalaiensis* (pers. observ., PM). A cone-chisel-shaped tooth from Ourém (Sauvage, 1897-98; Lapparent and Zbyszewski, 1957) is also related to Titanosauriformes, and the presence of some rotation of the apex suggest the assignation of this tooth to Brachiosauridae.

The lectotype of *Lourinhasaurus alenquerensis* (Moinho do Carmo, Alenquer) and *Lusotitan atalaiensis* (Peralta, Lourinhã) were recently revised. *Lourinhasaurus* was related to Camarasauridae (Mocho et al., 2014a) and *Lusotitan* seems to be a basal macronarian, and a brachiosaurid with doubt (Mannion et al., 2013).

In conclusion, the evaluation of this collection allow us to test the presence of eusauropods, (including turiasaurs), diplodocines, camarasaurids and basal titanosauriforms in the Portuguese Upper Jurassic. This is in accordance with the available data for the Portuguese Upper Jurassic sauropod faunas composed by the turiasaur *Zby atlanticus*, the diplodocid *Dinheirosaurus lourinhanensis* and several other diplodocid specimens, the camarasaurid *Lourinhasaurus alenquerensis* and the basal Macronarian, a possible brachiosaurid, *Lusotitan atalaiensis* (Rauhut et al., 2005; Whitlock, 2011; Mannion et al., 2012, 2013; Mocho et al., 2014a, b; Mateus et al., 2014). MG 4976 is preliminary related with the *Duriatitan humerocristatus*, an indeterminate eusauropod form from the British Upper Jurassic.

Museu Geológico collection also indicates the presence of a rich and diverse sauropod fossil record from the Upper Jurassic sediments including Alcobaça, Praia de Amoreira-Porto Novo, Sobral, Freixial and Bombarral Formations. This is also confirmed by other vertebrate groups (e.g. Sauvage, 1897-98; Lapparent and Zbyszewski, 1957; Galton, 1980; Pérez-Moreno et al., 1999; Rauhut, 2000; Antunes and Mateus, 2003; Escaso et al., 2007, 2010, 2014; Pérez-García and Ortega, 2011; Hendrickx and Mateus, 2014; Malafaia et al., 2010, 2015). This collection is one more argument to suggest that the West Portuguese region (Mafra, Torres Vedras, Lourinhã, Peniche, Alenquer, Caldas da Rainha, Leiria and Pombal) is one of the most productive territories in Upper Jurassic vertebrates of Europe.

5.6. CONCLUSIONS

Museu Geológico collections bear some of the first published occurrences on sauropods from the Upper Jurassic of the Lusitanian Basin, highlighting the studies of Sauvage (1897-98) and Lapparent and Zbyszewski (1957). The major part of the sauropod material housed in MG were collected in the 19th and during the first half of the 20th century, including the lectotype of *Lourinhasaurus alenquerensis* and *Lusotitan atalaiensis*. The most part of the fragmentary and isolated specimens were related to those taxa. Some authors noted for the importance to provide an accurate systematic revision (Dantas, 1990), and more recently, systematic revisions were proposed for *Lusotitan* and *Lourinhasaurus* lectotypes (Mannion et al., 2013; Mocho et al., 2014a). Nevertheless, for the more incomplete specimens the classical systematic approach remains (e.g. Antunes and Mateus, 2003; Mateus, 2005). We proposed a revised systematic context for most part of sauropod specimens housed in the Museu Geológico.

For the material previously related to *Lourinhasaurus alenquerensis* (MG 4799, 4800, 4802, 4804, 4976, 4978, 8800, 8805) the systematic approach was not confirmed and they correspond to indeterminate sauropods and eusauropods. For MG 4976, the presence of a proximodistal crest on the anterior face of the humeral proximal end allow us to a tentative assignation to the bristish taxa, *Duriatitan humerocristatus*, being the first occurrence of an Upper Jurassic sauropod shared between the Iberian Peninsula and United Kingdom. Nevertheless, *Duriatitan* is only based in a humerus, and the discovery of new specimens in both territories are necessary to test this hypothesis and the phylogenetic context of this taxon. MG 4800, 4986 and 8804 were previously related to *Lusotitan atalaiensis*, and only MG 8804 bears a putative autapomorphy of *Lusotitan atalaiensis*, the presence of two circular fossae behind the anterior articulation for the chevrons.

Some specimens collected in São Gregório da Fanadia (MG 4819, 4821, 4826) and Porto Novo (MG 25197.4-6) are tentatively related with the Dipldocinae clade. A specimen collected in Foz do Arelho (MG 4920) indicates the presence of sauropods with well-bifurcated neural spines on the Upper Jurassic of the Lusitanian Basin. The presence of bifurcated neural spines appears several times along the eusauropod evolutionary history but the fragmentary nature of this specimen only allow us to consider it as pertaining to an indeterminate eusauropod.

Finally, the material housed in the Museu Geológico suggest the presence of basal eusauropods (indeterminate eusauropods and turiasaurs) and neosauropods (indeterminate neosauropods, diplodocines, titanosauriforms) on the Portuguese Upper Jurassic, which is in accordance with the present known paleobiodiversity of this group for the Lusitanian Basin. It is also suggested the presence of shared forms (*Duriatitan*) between the Portuguese and British Upper Jurassic.

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CHAPTER 6

Sauropod tooth morphotypes recorded in the Upper Jurassic of the Lusitanian Basin (Portugal)

Sauropod tooth morphotypes recorded in the Upper Jurassic of the Lusitanian Basin (Portugal)

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6.1. INTRODUCTION

Upper Jurassic sediments of the Lusitanian Basin (Portugal) are known by abundant occurrences in fossil vertebrates, in particular, dinosaurs, turtles and crocodyliforms (e.g. Sauvage, 1897-98; Lapparent and Zbyszewski, 1957; Dantas, 1990; Antunes and Mateus, 2003; Ortega et al., 2006, 2008, 2013). The sauropod fossil record is particularly rich in this basin with several classical references (e.g. Sauvage, 1897-98; Lapparent and Zbyszewski, 1957) and from which it has been described four exclusive taxa: the camarasaurid *Lourinhasaurus alenquerensis* (Lapparent and Zbyszewski, 1957; Dantas et al., 1998; Mocho et al., 2014a); the diplodocid *Dinheirosaurus lourinhanensis* (Bonaparte and Mateus, 1999; Mannion et al., 2012), recently considered as a species of *Supersaurus* (Tschopp et al., 2015); the basal macronarian *Lusotitan atalaiensis*, a putative brachiosaurid with doubt (Lappatent and Zbyszewski, 1957; Antunes and Mateus, 2003; Mannion et al., 2013); and the turiasaur *Zby atlanticus* (Mateus et al., 2014).

The first sauropod teeth from of the Portuguese Upper Jurassic record were published by Sauvage (1897-98). They are two teeth from Fervença (MG 277) and Ourém (MG 16) referred to *Pelorosaurus humerocristatus*, and a second tooth (MG 8779) from Ourém referred to a new *Morosaurus* (=*Camarasaurus*) species, *Morosaurus marchei*. Sauvage (1897-98) also referred to this species a posterior caudal vertebra from Ourém (MG 4831) that actually does not belong to a sauropod (Lapparent and Zbyszewski, 1957), but recently considered as indeterminate theropod (Weishampel et al., 2004). *Morosaurus marchei* was considered as *nomina dubia* by Antunes and Mateus (2003), and MG 8779 was posteriorly related to an indeterminate macronarian (Mateus, 2005).

Lapparent and Zbyszewski (1957) revised and published several new dinosaur specimens from the Upper Jurassic of the Lusitanian Basin and from the Lower Cretaceous of Portugal. The tooth MG 8779 (Lapparent and Zbyszewski, 1957, pl. XXVIII, fig. 105A) was attributed to the species *Apatosaurus alenquerensis*, a taxon established from several occurrences highlighting the Moinho do Carmo (Alenquer) specimen. The Moinho do Carmo sauropod corresponds to the lectotype of *Lourinhasaurus alenquerensis* (Dantas et al., 1998; Antunes and Mateus, 2003) and no teeth were found in the type locality (Lapparent and Zbyszewski, 1957; Mocho et al., 2014a) being impossible to corroborate the original attribution of MG 8779 to this taxon. Another tooth housed (unnumbered) in the Museu Nacional de História Natural e da Ciência, (Lisboa) and figured by Lapparent and Zbyszewski (1957, pl XII, fig.1) was related to *Apatosaurus* sp. This tooth is not reachable in the these paleontological collections.

Only in the last part of the twentieth century new tooth occurrences have been reported, coincident in time with the renaissance of the research on the vertebrate faunas of the Portuguese Upper Jurassic record (e.g. Dantas, 1987, 1990; Dantas et al., 1992, 1998; Mateus et al., 1997; Mateus, 1998; Bonaparte and Mateus, 1999; Rauhut, 2000; Antunes and Mateus, 2003). From Guimarota mine, some sauropod teeth were recovered and related to Brachiosauridae, despite the absence of another skeletal specimens attributable to sauropods in the locality (Thulborn, 1973; Rauhut, 2000). The first teeth found associated to a partial skeleton (ML 368) in the Lusitanian Basin Upper Jurassic correspond to a specimen firstly related to *Camarasaurus* sp. (Mateus, 2005), later considered as *Turiasaurus riodevensis* (Mateus, 2009), and finally described as a new turiasaur sauropod, *Zby atlanticus* (Mateus et al., 2014). Several authors noted for the affinities of this specimen to the Turiasauria clade, including the heart-shaped morphology of the preserved tooth (Mateus, 2009; Royo-Torres et al., 2009, 2014a; Mocho et al., 2012, in press; Royo-Torres and Upchurch, 2012), considered as a synapomorphy of this clade (Royo-Torres et al., 2006, 2009; Mocho et al., 2012, in press; Royo-Torres and Upchurch, 2012). Several other teeth from the Upper Jurassic sediments of the Lusitanian Basin were tentatively related with clade (Royo-Torres et al., 2009; Malafaia et al., 2010; Ortega et al., 2010; Mocho et al., 2012, in press; Royo-Torres and Upchurch, 2012) and three different heart-shaped morphotypes were proposed based on their morphological variability (Mocho et al., 2012, in press).

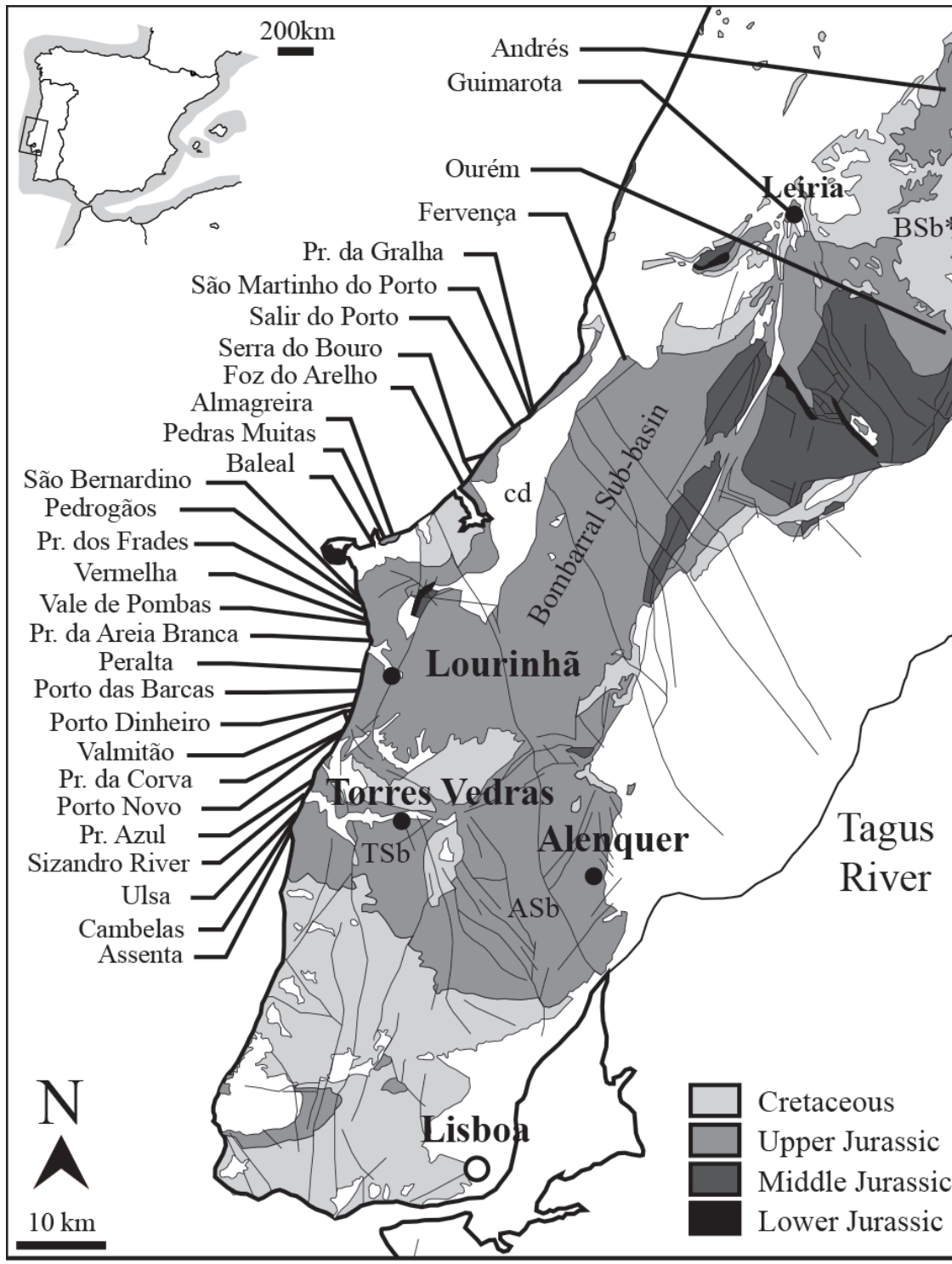


Figure 6.1. Geological map (adapted from Oliveira et al., 1992) showing the Portuguese Mesozoic levels and the localities where was found sauropod teeth on the Lusitanian Basin. ASb- Arruda Sub-basin; BSb – Bombarral Sub-basin, cd – Caldas Diapir; TSb – Turcifal Sub-basin.

At the Andrés locality (Bombarral Formation, Tithonian, see Fig. 6.1 for location) was recognized a great accumulation of a relatively diverse fauna of vertebrates (Dantas et al., 1999; Pérez-Moreno et al., 1999; Malafaia et al., 2007, 2009, 2010). In the Andrés quarry were collected teeth and postcranial material assigned to Sauropoda and a preliminary analysis identified three distinct tooth morphotypes: spoon-, chisel- and pencil-shaped teeth, suggesting for the presence of indeterminate diplodocoids, titanosauriforms and, tentatively, turiasaurs (Malafaia et al., 2010). Mocho et al. (2011) also referred the presence of spatulate-shaped teeth from Peralta (Lourinhã) and Cambelas (Torres Vedras) discussing their assignment to Euhelopodidae or Camarasauridae.

A significant sample of sauropod teeth from the Upper Jurassic of the Lusitanian Basin housed in Sociedade de História Natural, Museu Geológico and Museu National de História Natural e da Ciência is described and discussed herein, including classical and unpublished specimens. The recognized morphotypes will be contrasted with the known paleobiodiversity for the Portuguese Upper Jurassic sauropod faunas (e.g. Lapparent and Zbyszewski, 1957; Dantas et al., 1998; Bonaparte and Mateus, 1999; Antunes and Mateus, 2003; Yagüe et al., 2006; Mannion et al., 2012, 2013; Mocho et al., 2013a, b, 2014a, b; Mateus et al., 2014).

6.2. GEOLOGICAL SETTINGS

The Upper Jurassic beds in the Lusitanian Basin are dated from the middle Oxfordian to the base of the Cretaceous (Fig. 6.2) (Schneider et al., 2009), and represents a third rifting episode (Rasmussen et al., 1998; Kullberg et al., 2006) marked by an internal differentiation resulting in the formation of several sub-basins (Turcifal, Arruda and Bombarral Sub-basins) followed by an important siliciclastic input which progressively infilled these sub-basins (Hill, 1988; Pena dos Reis et al., 2000; Kullberg et al., 2006). Since the Kimmeridgian, the sedimentary sequence is markedly siliciclastic, with a continental signature in the top of the sequence (e.g. Hill, 1988; Manuppella et al., 1999; Kullberg et al., 2006). Different stratigraphic approaches have been proposed for the Upper Jurassic sequence of these sub-basins (e.g. Hill, 1988; Leinfelder, 1993; Manuppella et al., 1999; Kullberg et al., 2006; Schneider et al., 2009; Martinius and Gowland, 2011; Taylor et al., 2013, see Fig. 6.2). The described occurrences come from the Upper Jurassic sediments outcropping at the coastal cliffs extended from Assenta to São Martinho do Porto (incorporated in the Bombarral Sub-basin, following Kullberg et al., 2006, or Consolação Sub-basin following Taylor et al., 2013), and from Ourém, Fervença, Andrés and Guimarota from the central and north sector of the Bombarral Sub-basin (Fig. 6.1). They were identified in Alcobaça, Praia de Amoreira-Porto Novo, Sobral, Bombarral and Freixial Formations.

6.3. ANATOMICAL ABBREVIATIONS

Awf, apical wear facet; bwf, wear facet at the base of the crown; cwf, carina wear facet; env, external nares ventral margin; etc, erupted tooth crown; etr, erupted tooth row; lag, labial groove; lb, lateral bulge; lf, lingual facet; lic, lingual crest; mr, labial mesial at the base of the crown; rb, round boss; rtc, replacement tooth crown; SI, slenderness index; "v" wf, v-shaped wear facet.

6.4. INSTITUTIONAL ABBREVIATIONS

HMN, Humboldt Museum für Naturkunde, Berlin, Germany; ML, Museu da Lourinhã, Lourinhã, Portugal; MG, Museu Geológico do Laboratório Nacional de Energia e Geologia, Lisboa, Portugal; MUJA, Museo del Jurásico de Asturias, Asturias, Spain; SHN, Sociedade de História Natural, Torres Vedras, Portugal (plus (JJS) for the José Joaquim dos Santos collection deposited in the Sociedade de História Natural).

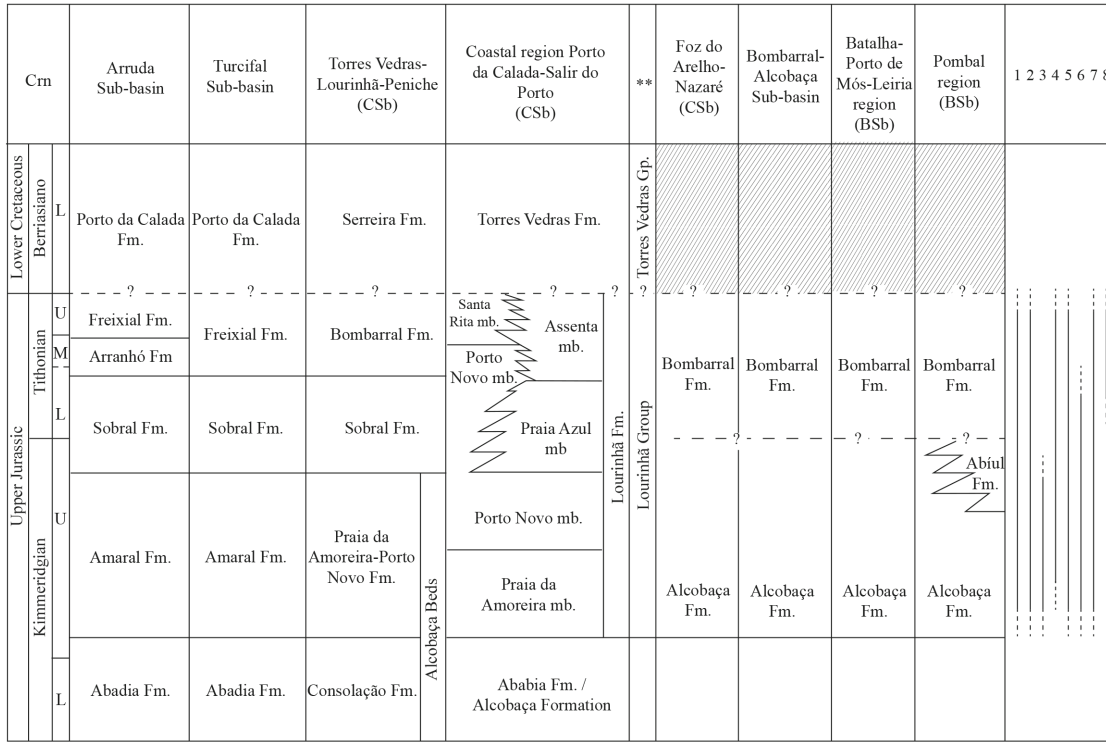


Figure 6.2. Stratigraphic correlation between the nomenclature proposed for *i*) Turcifal Sub-basin (based on Pereda-Suberbiola et al., 2005; Kullberg et al., 2006; Schneider et al., 2009), *ii*) Arruda Sub-basin (Kullberg et al., 2006); *iii*) Consolação Sub-basin areas: Torres Vedras-Lourinhã-Peniche (based on Manuppella et al. 1999), Foz do Arelho-Nazaré coastal sector (Kullberg et al., 2006; Azerêdo et al., 2010); *iv*) Bombarral-Alcobaça Sub-basin (based on Azerêdo et al., 2010); *v*) Batalha-Leiria region (based on Manuppella et al., 2000; Kullberg et al., 2006; Escaso et al., 2007) and *vi*) Pombal region (Kullberg et al., 2006; Malafaia et al., 2010). The stratigraphy proposed by Hill (1988) for the coastal sector from Porto da Calada to Salir do Porto is also plotted. Crn – Chronostratigraphy; ***sensu* Yagüe et al., 2006. The right column show the known stratigraphic distribution for the described morphotypes herein and in Mocho et al. (in press): Heart-shaped teeth (1- morphotype I; 2- morphotype II; 3- morphotype III), spatulate shaped teeth (4); compressed cone-chisel-shaped teeth (5 – morphotype I; 6 – morphotype II; 7 – morphotype III), and pencil-shaped teeth (8). BSb, Bombarral Sub-basin (following Kullberg et al., 2006); CSb, Consolação Sub-Basin (following Taylor et al., 2013).

6.5. SAUROPOD TOOTH MORPHOTYPES

More than 60 teeth coming from several localities on the Bombarral (Consolação and Bombarral-Alcobaça Sub-basins following Taylor et al., 2013) and Turcifal Sub-basins (Figs. 6.1, 6.2) are described and discussed herein. According with main tooth morphotypes present in sauropods (e.g. Calvo, 1994; Upchurch and Barrett, 2000; Upchurch et al., 2004; Royo-Torres et al., 2006; Mocho et al., 2012) we will divided our sample in heart-, pencil-, spatulate-, and compressed cone-chisel-shaped teeth. For some of these main categories, can be defined several morphotypes, as it was previously proposed by Mocho et al. (2012, in press) for heart-shaped teeth.

6.5.1. Heart-shaped teeth

Material: 43 heart-shaped teeth were described and discussed by Mocho et al. (2012, in press) and a maxilla fragment preserving teeth is herein reported (Fig. 6.4). Several aspects about the wrinkled texture of these heart-shaped teeth are also commented.

Description: These teeth were described in detail by Mocho et al. (2012, in press). The crown has a heart-shaped morphology, compressed labiolingually and present a wrinkled texture on the enamel. In general, the base of the crown is slightly apicomesially projected and the teeth reach the maximum mesiodistal width near the base of the apex. Excluding the more worn teeth, the slenderness index (crown height/maximum crown breadth, *sensu* Upchurch 1998) ranges between 1.1 and 1.8.

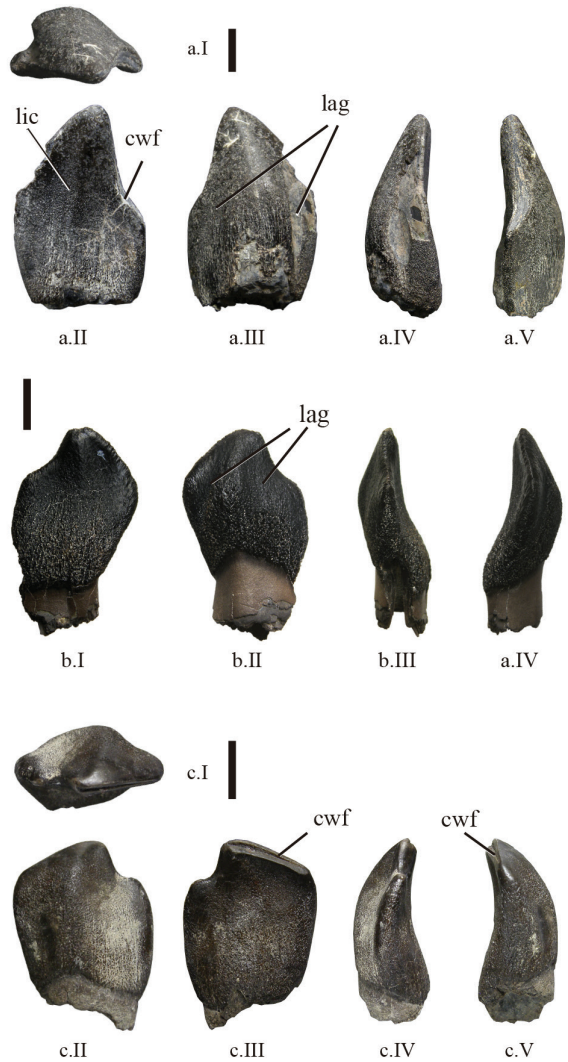


Figure 6.3. Heart-shaped teeth from the Upper Jurassic of the Lusitanian Basin. Morphotype I, SHN (JJS) 142 (Praia da Corva) in apical (a.I), lingual (a.II), labial (a.III), mesial (a.IV) and distal (a.V) views. Morphotype II, SHN 144 (Porto Dinheiro) in lingual (b.I), labial (b.II), distal (b.III) and mesial (b.IV) views. Morphotype III, SHN 137 (São Bernardino) in apical (c.I), labial (c.II), lingual (c.III), distal (c.IV) and mesial (c.V) views Scale bar: 10mm.

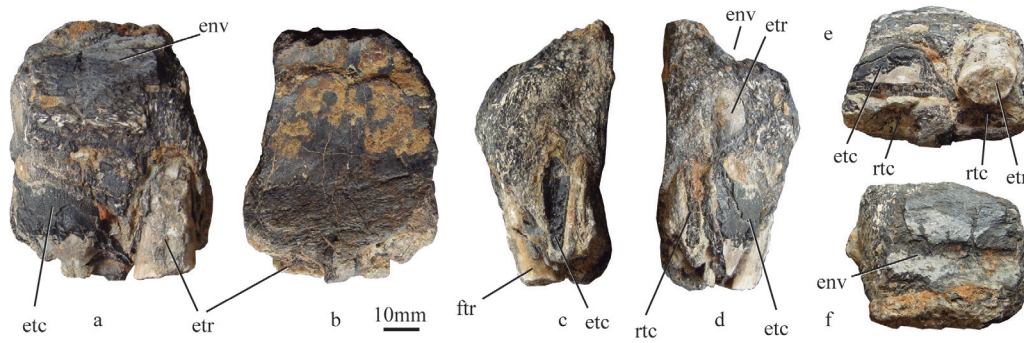


Figure 6.4. Partial left maxilla (SHN 582) with heart-shaped teeth from Praia dos Frades in lateral (a), medial (b), posterior (c), anterior (d), ventral (e) and dorsal (f) views. Scale bar: 10mm.

On the labial face, the teeth display an apicobasal bulge bounded by shallow grooves with the same orientation. The lingual face has a low ridge, which extends along all the apicobasal length of the face. The mesial and distal edges are not parallel and diverge from the base of the tooth. The transition between the row and the crown is well-marked in all teeth. The teeth exhibit asymmetrical D- to lenticular-shape cross-section, with a strong convexity in labial face and a flat-to-smooth concave lingual face. The maximum labiolingual width is located near the mesial edge, resulting in a steeply angled mesial part on the labial surface. The asymmetrical apex deflects distally. In labial/lingual view, the mesial and distal edges of the apex are straight to slightly convex and concave, respectively. Generally, the distal edge of the apex is longer than the mesial one (excluding the morphotype III, see Mocho et al., in press). Crown-to-crown occlusion produced V-shaped wear facets. Mocho et al. (2012, in press) described three different morphotypes (see Fig. 6.3): *morphotype I*) significant SI (1.8-1.6) values and high apex (an half of the tooth total height), *morphotype II*) moderate apex and SI values (1.5-1.3), with well defined heart-shaped and more strong distal deflection of the apex; *morphotype III*) low SI values (<1.3) and extremely low apex, crowns with heart-shaped to subsquare-shaped outline.

In this study we also describe a skull fragment (SHN 582, Fig. 6.4) found in Praia dos Frades (Peniche), this is the first sauropod no dental cranial specimen so far described from the Lusitanian Basin. Comparing with other sauropod skulls (Janensch, 1936; Madsen et al., 1995; Poropat et al., 2013; Marpmann et al., 2015) and according with the slight imbrication that presets the associated tooth row, this fragment is tentatively interpreted herein as a partial left maxilla. The specimen preserves the ventral border of the external nares. The border is medially emarginated, becoming subhorizontal and separated from the maxilla lateral face by a longitudinal crest. The maxilla presents a smooth medial surface, and the available sector does not preserve foramina neither the alveoli border. On this fragment is possible to observe, laterally, the tooth row with three erupted teeth (if they are functional or non-functional is unknown): a tooth crown, an almost complete crown (lacking part of the apex) and the mesial border of a third tooth crown. In this fragment is also possible to recognize two replacing teeth, one for alveoli.

Texture: The wrinkled texture of the three morphotypes defined by Mocho et al. (in press) will be described in detail herein (Fig. 6.5). In the morphotype I, the labial surface presents several changes along the crown. On the bulge area, and near the base of the crown, the texture is composed by apicobasal ridges that can branch out generating secondary ridges. Near the mesial and distal edges of the crown, these ridges become apicobasally shorter and the ridges give rise to a scale-like structures (with subtriangular morphology). The pattern on the lingual face is similar: wrinkled texture composed by short ridges on the center and the base of the crown, being replaced by scale-like structures close to the apex and close to the edges of the crown base (Fig. 6.5b, c). Close to the transition between the crown and the root, the ridges also are scale-shaped. The scale-shaped

structures are mesial or distal deflected in the mesial and distal edge of the crown, respectively (Fig. 6.5b, c). A similar pattern is also observed in teeth assigned to the morphotype II (Fig. 6.5f-g, i-m, o-p). In the morphotype III, only some specimens present a wrinkling pattern composed by ridges (SHN (JJS) 128). The texture is dominated by scale-like structures also deflecting close to the mesial and distal edges of the crown (Fig. 6.6). Wear might affect the wrinkling pattern on the apex region or on the edges of the crown base, and in some cases, it is possible to identify a surface of abrasion close to the wear facets (Figs. 6.5a, k, m, p, 6.6i).

Wear pattern: Mocho et al. (in press) propose that, in the morphotypes I and II, the wear pattern begins with a distal facet, after a mesial/apical facet and later a V-shaped facet. In morphotype III the wear starts with a mesial facet.

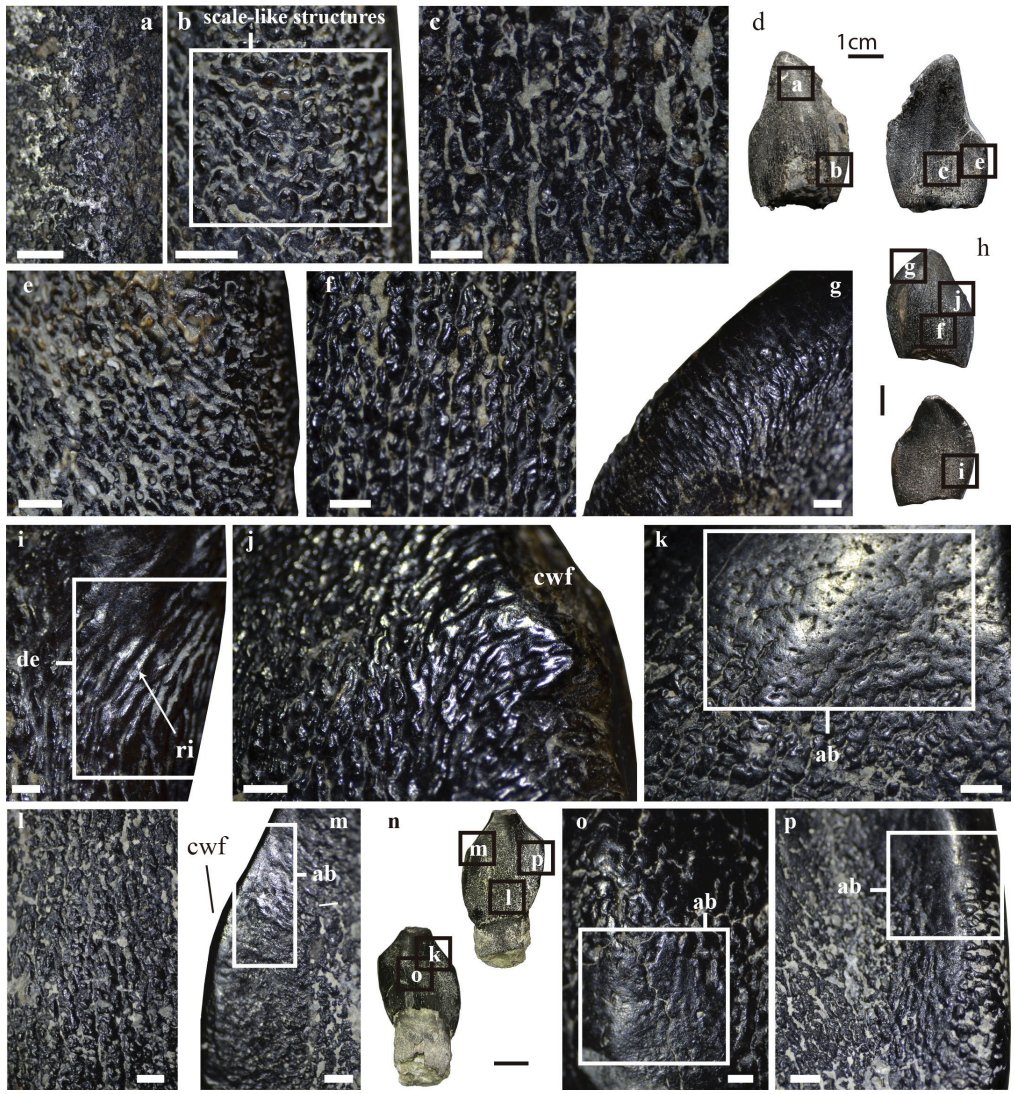


Figure 6.5. Wrinkling pattern in the morphotype I and II of heart-shaped teeth. The position of each photo is indicated on d (SHN (JJS) 142), h (SHN 138) and n (SHN (JJS) 141). a, b, c, e: wrinkling pattern of SHN (JJS) 142 (Praia da Corva, morphotype I); f, g, i, j: wrinkling pattern of SHN 138 (Porto Novo, morphotype II); k, l, m, o, p: wrinkling pattern of SHN (JJS) 141 (Baleal, morphotype II). Black scale bar: 10mm; white scale bar: 1mm. ri – ridge; ab – abrasion.

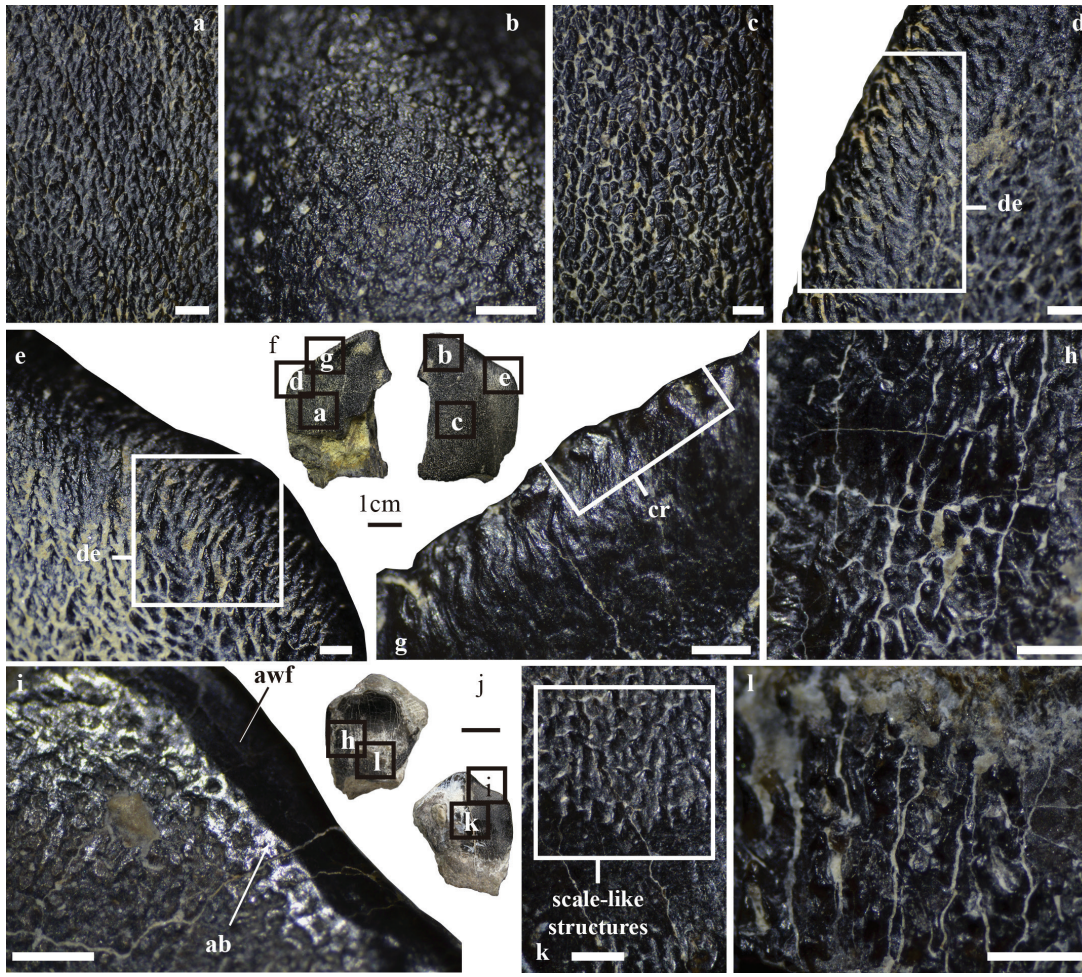


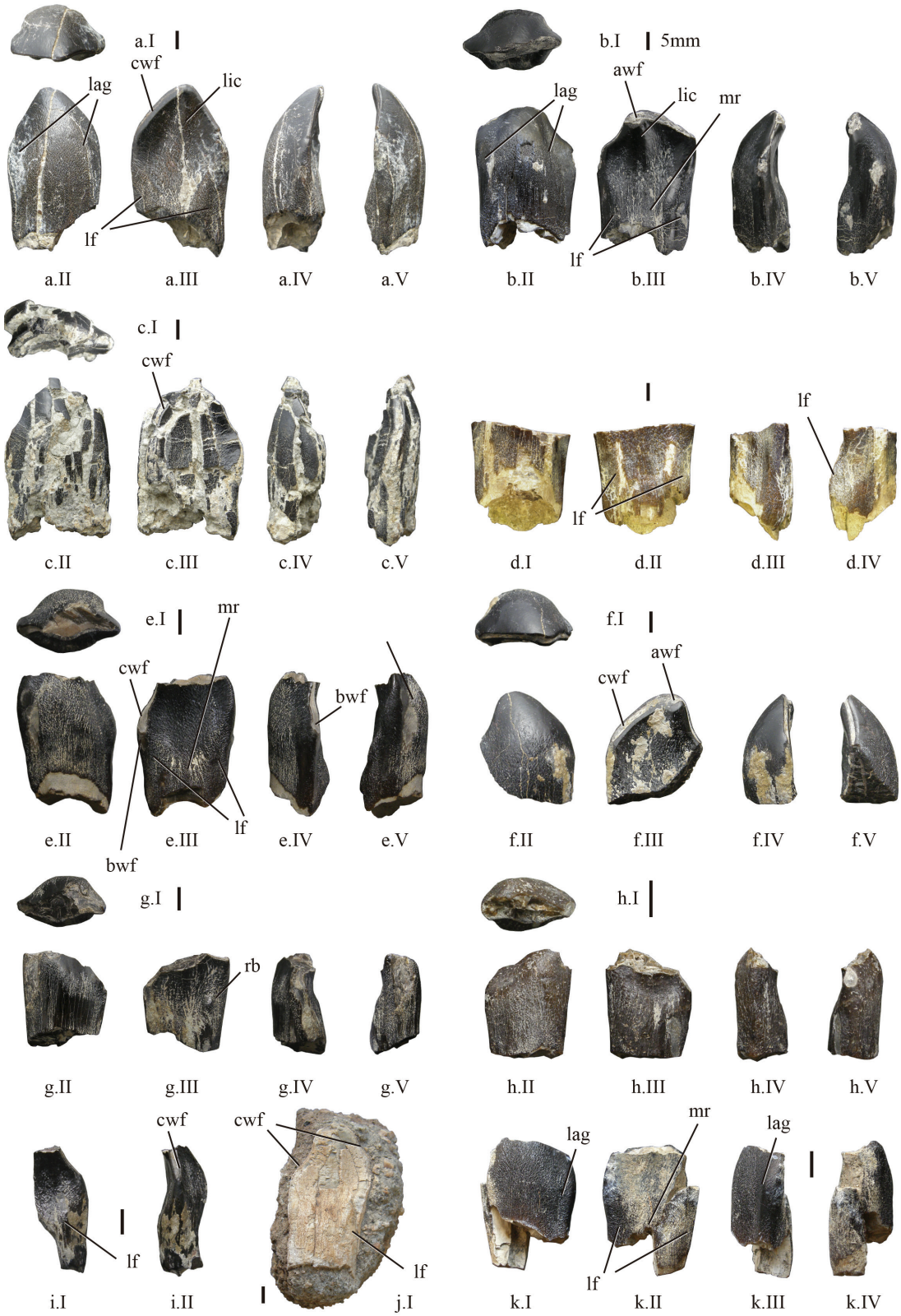
Figure 6.6. Wrinkling pattern on the morphotype III of heart-shaped teeth. The position of each photo is indicated on f (SHN (JJS) 146), j (SHN (JJS) 149). a-e, g: wrinkling pattern of SHN (JJS) 146 (Salir do Porto, morphotype III); h, i, k, l: wrinkling pattern of SHN (JJS) 149 (unknown locality, morphotype III). Black scale bar: 10mm; white scale bar: 1mm. de – ridge/scale deflection; cr – crenulation on the apex; ri – ridge; ab – abrasion.

6.5.2. Spatulate-shaped teeth

Material: Eleven complete to partial spatulate-shaped teeth: SHN 121, 122, 513-519, 540-41 and MG 8783 (Figs. 6.7, 6.8).

Locality and horizon: Several localities at Caldas da Rainha, Peniche, Lourinhã and Torres Vedras municipalities (see S.4) in sediments belonging to Praia de Amoreira-Porto Novo, Sobral, Freixial and Bombarral Formations, and resulting in a stratigraphic range from upper Kimmeridgian to Tithonian (Fig. 6.2; Manuppela et al., 1999; Kullberg et al., 2006; Azerêdo et al., 2010).

Description: Although the presence of some morphological disparity, the morphological variability on the present sample is not so significant than in the heart-shaped morphotype and we will not propose a subdivision into distinct morphotypes.


a.I
cwf
lag
lic
lf
a.II
a.III
a.IV
a.V
b.I
5mm
awf
lag
lic
mr
lf
b.II
b.III
b.IV
b.V
c.I
cwf
c.II
c.III
c.IV
c.V
lf
d.I
d.II
d.III
d.IV
e.I
mr
cwf
bwf
lf
bwf
e.II
e.III
e.IV
e.V
f.I
awf
cwf
f.II
f.III
f.IV
f.V
g.I
rb
g.II
g.III
g.IV
g.V
h.I
h.II
h.III
h.IV
h.V
cwf
lf
i.I
i.II
cwf
lf
j.I
lag
mr
lf
k.I
k.II
lag
k.III
k.IV

One of the most complete teeth (SHN 122, previously referred as ALT. SHN 122 by Mocho et al., 2011, Fig. 6.7a) was collected in the Sobral Formation at the Peralta coastal cliffs. SHN 122 is interpreted as a probably premaxillary or maxillary tooth because it has a lingual wear. It is a spatulate-shaped tooth, with a wrinkled enamel and D-shaped cross-section. The labial face is strongly convex mesiodistally bearing a well-developed apicobasal bulge bordered by two smooth apicobasal grooves more pronounced at the base. This apicobasal bulge is pronounced up to the apex of the crown and more inflated and globose than the labial bulge present in the heart-shaped teeth (Fig. 6.3). The lingual face of the crown is concave mesiodistally and apicobasally (deeper on the apex) and bears an apicobasal crest in the apex. The mesial edge of the base of the crown is straight and the distal one is slightly concave. Both edges are parallel in its first two thirds of the crown. On the lingual face, in the mesial and distal edges of the crown base, there are leaf-shaped lingual facets (Fig. 6.7a.III) resulting in a complex cingulum. These facets are well separated from the lingual face by the presence of pronounced ridges. These facets are pronounced and similar in SHN 513, 514, 515, 517 519 and MG 8783, but smoother in SHN 518 and 540-41 (Fig. 6.7b.III, d.II, e.III, g.III, h.III, i.I, j.I and k.II). Apically, the edges converge forming an almost symmetric apex, with a slight distal deflection. The teeth in more advanced stages of wearing bear a V-shaped wear facet resulting from crown-to-crown occlusion. SHN 513 from Porto Novo (Torres Vedras, Fig. 6.7b) is almost complete, and presents the same general morphology, but with signs of a more pronounced abrasion/erosion of the crown. On the studied sample, the distal deflection of the apex is variable, being almost symmetrical in SHN 122 (Fig. 6.7a) and distally deflected in SHN 121 (Fig. 6.7f), SHN 513 (Fig. 6.7b), SHN 519 (Fig. 6.7j), and probably SHN 517 (Fig. 6.7e). Differences on the deflection of the apex might be related with its position on the tooth row as occur in other sauropods, becoming more pronounced when are placed more distally in the tooth row (e.g. Osborn and Mook, 1921; Ostrom and McIntosh, 1966; Madsen et al.,1995; Ouyang and Ye, 2002; Wilson and Upchurch, 2009; Poropat et al., 2013; Holwerda et al., 2015).

SHN 514, 517 and 519 present some different aspects when compared to SHN 513 or 122. They present a mesial imbrication. This feature also occurs in the more distal teeth of *Camarasaurus lentus* (Gilmore, 1925) or *Euhelopus* (Wilson and Upchurch, 2009; Poropat et al., 2013). The lingual apicobasal crest is pronounced on the apex and on the base of the crown, becoming smooth at mid-height of the crown (e.g. Fig. 6.7e). In SHN 541 (Fig. 6.7g) is not possible to test the presence of a mesial imbrication, nevertheless, a pronounced lingual apicobasal crest at the base of the crown suggests that SHN 541 probably shares a similar morphology with SHN 514, 517 and 519. The ridge bordering the mesial lingual facet of SHN 541 bears a rounded boss (Fig. 6.7g.III), resembling the rounded bosses present in *Euhelopus* (Wilson and Upchurch, 2009) and in other Asiatic Lower Cretaceous teeth (Suteethorn et al., 2013). The SI of the present sample ranges between 1.9 and 1.5.

Figure 6.7. Spatulate-shaped teeth from the Upper Jurassic of the Lusitanian Basin. SHN 122 (Peralta) in apical (a.I), labial (a.II), lingual (a.III), mesial (a.IV) and distal (a.V) views. SHN 513 (Porto Novo) in apical (b.I), labial (b.II), lingual (b.III), distal b.IV) and mesial (b.V) views. SHN 515 (Peralta) in apical (c.I), labial (c.II), lingual (c.III), mesial (c.IV) and distal (c.V) views. MG 3783 (Baleal) in labial (d. I), lingual (d.II), distal (d.III) and mesial (d.IV) views. SHN 517 (Foz do Arelho) in apical (e.I), labial (e.II), lingual (e.III), distal (e.IV) and mesial (e.V) views. SHN 121 (Cambelas) in apical (f.I), labial (f.II), lingual (f.III), mesial (f.IV) and distal (f.V) views. SHN 541 (south of Pedra da Ulsa) in apical (g.I), labial (g.II), lingual (g.III), distal (g.IV) and mesial (g.V) views. SHN 540 (São Bernardino) apical (h.I), labial (h.II), lingual (h.III), mesial (h.IV) and distal (h.V) views. SHN 518 (Peralta) in lingual (i.I) and distal (i.II) views. SHN 519 (South of Foz do Sizandro) in lingual (j.I) view. SHN 514 (Serra do Bouro) in labial (k.I), lingual (K.II), mesial (k.III) and distal (k.IV) views. Scale bar: 5mm.

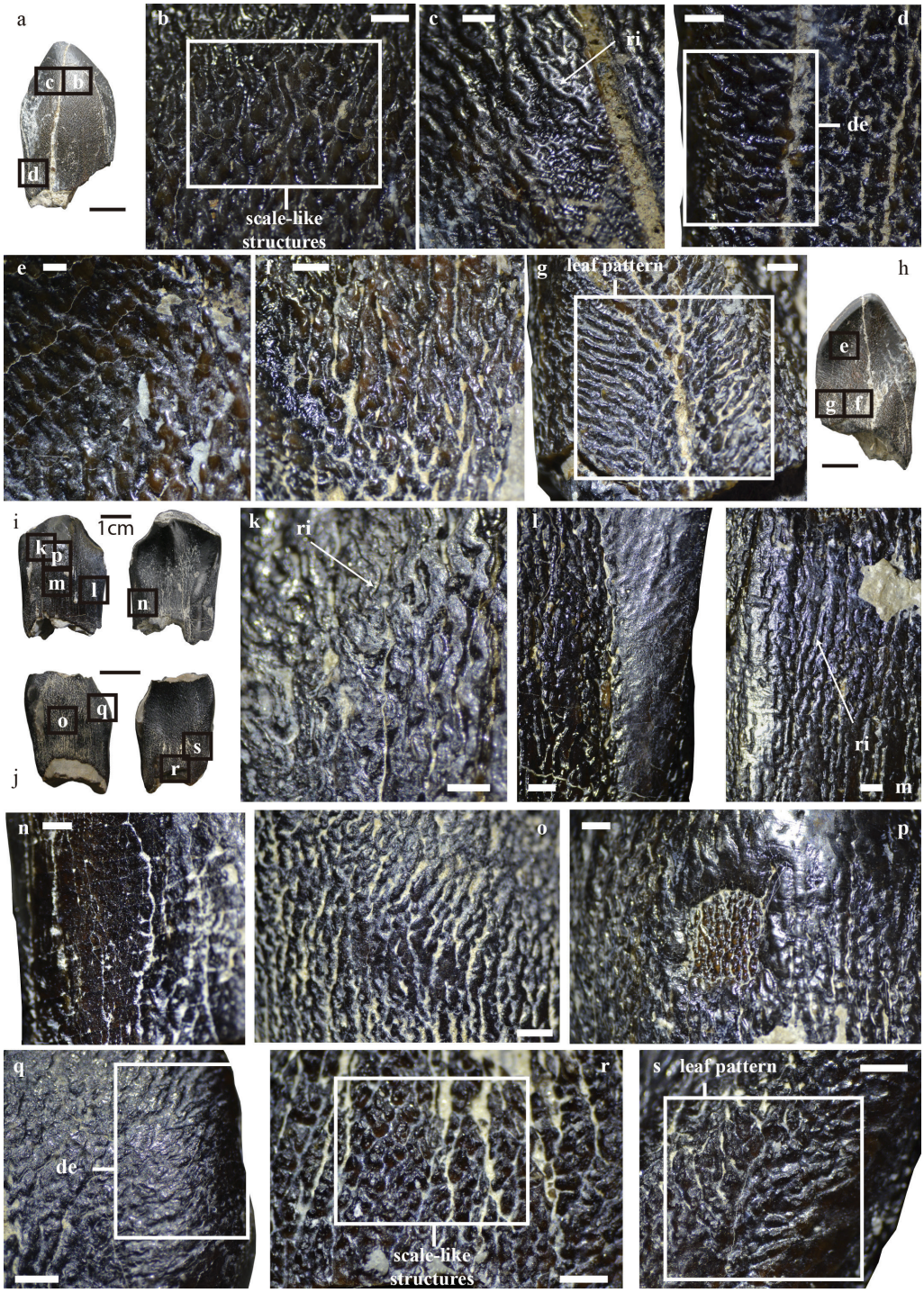


Figure 6.8. Wrinkling pattern on spatulate-shaped teeth from the Upper Jurassic of the Lusitanian Basin. The position of each photo is indicated on a and h (SHN 122), i (SHN 513) and j (SHN 517). b-f: wrinkling pattern of SHN 122 (Peralta); k-n, p: wrinkling pattern of SHN 513 (Porto Novo). o, q-s: wrinkling pattern of SHN 517 (Foz do Arelho). Black scale bar: 10mm; white scale bar: 1mm. de – ridge/scale deflection; ri – ridge.

Texture: The wrinkling pattern of enamel is similar to pattern present in other spatulate-shaped teeth (e.g. *Camarasaurus*). It is marked by an alternation between apicobasal and waved grooves and anastomosed ridges. In the lingual and labial face, the texture is composed by well-defined ridges, connected by secondary ridges, which results from the bifurcation of the main ones (Fig. 6.8b, f, m, k). In some cases, this ornamentation becomes locally thinner and acquires a reticular morphology (Fig. 6.8c). Close to the edge of the crown, the ridges deflect toward the edge (Fig. 6.8d, l, q). Close to the apex and on the lingual facets, the ridges are not so well defined and the wrinkled texture is composed mainly by superimposed scale-like structures (Fig. 6.8o, r, q) similar to the ornamentation present in the heart-shaped teeth (Figs. 6.5, 6.6). These scale-like structures has wider distribution on the enamel surface in smaller teeth, suggesting some ontogenetic or positional variability if this morphotype comes from the same species. On the lingual facets, the ridges/scales are confluent to the sagittal axis of this facet, i.e. the distributions of the ridges/scales resembles the veins of a leaf (Fig. 6.8g, s). The areas close to the apex and to the wear facets are generally polished (Fig. 6.8n, p-q) and the ornamentation becomes smoother. In some teeth, the ridges that compose the ornamentation are clearly truncated by the abrasion, and in some cases they could be absent (Fig. 6.8k, l, n).

Wear pattern: The present sample of Portuguese Upper Jurassic spatulate-shaped teeth is not so abundant, but it is possible to make some inferences about the wear pattern present in this type of teeth. SHN 122 is the less worn tooth, and the mesial wear facet is almost vertical. The distal edge of the apex is free of wear (Fig. 6.7a.III), suggesting that the wear in this morphotype probably starts in the mesial edge as occur in hearts-shaped teeth (Mocho et al., in press). In teeth with the mesial edge in more advanced stage of wear (e.g. SHN 121, 515, 519), it is also possible to observe the presence of a distal wear facet with a lingual slope (Fig. 6.7c, f, j). On the other hand, the mesial wear facet always slopes lingually, in our sample. In more advanced stages, an apical wear facet appears, and the mesial one loses progressively the lingual slope (Fig. 6.7b, SHN 513). A distal local round wear facet on the transition between the apex and the base of the crown is also present (Fig. 6.7b, SHN 513; Fig. 6.7e, SHN 51; Fig. 6.7h, SHN 540) in connection with the distal wear facet.

In conclusion, with the available sample can be interpreted a sequence of wear for the spatulate-shaped teeth. The wear pattern begins with a distal facet, after a mesial facet and later an apical facet. In more progressive stages of wear, a round distal wear facet on the transition between the apex and the crown base might appear. The apex in teeth with an advanced wear also presents a significant abrasion in the apex (e.g. SHN 513), and in some cases, some evidences of abrasion are also present in base of the crown (Fig. 6.7g, SHN 541; Fig. 6.7h, SHN 540).

Discussion: These teeth bear an enamel with a wrinkled texture, crown overlapping, spatulate-shaped crowns and V-shaped wear facets. These characters were considered as synapomorphies of Eusauropoda (Wilson and Sereno, 1998), but seems to appear sooner in the sauropod evolutionary history, being present in some non-eusauropod sauropods (e.g. Allain and Asquebi, 2008; Carballido and Pol, 2010). The spatulate-shaped morphology of these teeth shows considerable morphological affinities with *Camarasaurus* and *Euhelopus* teeth (e.g. Marsh, 1878; Osborn and Mook, 1921; Gilmore, 1925; Wiman, 1929; Ostrom and McIntosh, 1966; Madsen et al., 1995; McIntosh et al., 1996a, b; Wilson and Upchurch, 2009) and some eusauropods such as *Omeisaurus* or *Mamenchisaurus* (He et al., 1988; Ouyang and Ye, 2002; Suteethorn et al., 2013), which might form a monophyletic clade, Mamenchisauridae (Sekiya, 2011; Mannion et al., 2013; Suteethorn et al., 2013; Carballido and Sander, 2014).

The spatulate-shaped teeth are characterized by straight and subparallel distal and mesial edges in the base of the crown, and by the presence of convex labial and concave lingual faces (e.g. *Camarasaurus*, *Euhelopus*, Mamenchisauridae, *Omeisaurus*). They differ from the heart-shaped teeth in several ways: *i*) higher SI values (1.53– 2.447 *sensu* Chure et al., 2010); *ii*) distal

and mesial edges are straight and almost parallel in the base of the crown, *iii*) shorter apices; *iv*) bear lingual facets and a marked and complex cingulum on the lingual face; *v*) a lingual crest that general appears only in the apex sector; *vi*) absence of heart-shaped morphology; *vii*) lingual projection of apex more pronounced than heart-shaped teeth; *viii*) the labial face of the apex is more inflated and globose.

The occurrence of spatulate-shaped teeth in several taxa phylogenetically unrelated (Wilson, 2002; Upchurch et al., 2004; D'Emic, 2012; Mannion et al., 2013; Carballido and Sander, 2014) suggests that this morphology was obtained several times in sauropod evolution, being present in euhelopodids, camarasaurids and mamenchisaurids (e.g. Gilmore, 1925; Wiman, 1929; He et al., 1988), showing high plasticity of sauropod teeth (Upchurch et al., 2007; Carballido and Pol, 2010). "*Chiayusaurus lascustris*" teeth (considered as *nomima dubia* by McIntosh 1990a, and as "*Asiatosaurus mongoliensis*" by Barrett et al., 2002); and teeth figured by Averianov et al. (2005, fig. 5) from the Middle Jurassic of Balabansai Svita (Kyrgyzstan) seem to share the same spatulate camarasaurid-shaped tooth morphology. In the Kyrgyzstan teeth, there are denticulation that might relate it with Mamenchisauridae.

The presence of rounded lingual bosses was considered an autapomorphy of *Euhelopus* teeth (Wilson, 2002; Barrett and Wang, 2007; Wilson and Upchurch, 2009). Based in the presence of this character, Canudo et al. (2002) referred a tooth from Lower Cretaceous of Teruel (Spain) as Euhelopodidae. These rounded bosses was also identified in some teeth collected from Lujiatun Beds of the Yixian Formation (Aptian) of Lujiatun, in the Chinese Province of Liaoning (Barrett and Wang, 2007), and on the recently published Asian titanosaur, *Yongjinglong datangi* (Li et al., 2014).

Suteethorn et al. (2013) refer the presence of lingual bosses in *Mamenchisaurus* (Russell and Zheng, 1993; Ouyang and Ye, 2002), *Omeisaurus* (He et al., 1988), *Euhelopus* (Wiman, 1929), *Camarasaurus* (e.g. Osborn and Mook 1921) and in isolated teeth from Thailand (Buffetaut and Suteethorn 2004) and Spain (Canudo et al., 2002). Those authors do not discriminates the rounded bosses present in *Euhelopus* (Wilson and Upchurch, 2009) from the lingual facets common in spatulate-shaped teeth. Herein, we referred as lingual facets, the individualized leaf-shaped facets present on the lingual face near mesial and distal edges of the crown base. These facets are present in several taxa with spatulate-shaped teeth such as *Mamenchisaurus* (Ouyang and Ye, 2002), *Omeisaurus* (He et al., 1988), *Euhelopus* (Wiman, 1929), *Camarasaurus* (e.g. Marsh, 1878; Osborn and Mook, 1921; Gilmore, 1925; Ostrom and McIntosh, 1966; Madsen et al., 1995; McIntosh et al., 1996a, b), *Yongjinglong datangi* (Li et al., 2014) and *Euhelopus* (Wiman, 1929; Wilson and Upchurch, 2009; Suteethorn et al., 2013) and not so well-developed in *Giraffatitan* (pers. observ., PM). The rounded bosses present in *Euhelopus* (Wilson and Upchurch, 2009) are small bosses associated to the borders of the lingual facets. This kind of structures are present in SHN 541, and were considered as an autapomorphy of *Euhelopus* (Wilson and Upchurch, 2009). The lingual facets of SHN 122 are bordered by pronounced ridges as occur in some teeth of *Camarasaurus* (e.g. Marsh, 1878; Osborn and Mook, 1921; Gilmore, 1925; Ostrom and McIntosh, 1966; Madsen et al., 1995; McIntosh et al., 1996a, b). These ridges were misidentified as rounded bosses by Mocho et al. (2011). The redescription of this specimen allow concluding that SHN 122 does not bear round bosses as *Euhelopus*.

Suteethorn et al. (2013) discriminate *Euhelopus* and *Camarasaurus* from *Omeisaurus*, *Mamenchisaurus* and some Thailand teeth. One former taxa, belonging to the Macronarian clade, might present one or two lingual facets associated to the cingulum and in some cases, a medial ridge. The described variability for the cingulum in those taxa is also present in our sample: one developed facet (Fig. 6.7h, SHN 540), two well-developed facets (Fig. 6.7a, SHN 122) and two facets more a medial ridge (Fig. 6.7e, SHN 517). *Omeisaurus* and *Mamenchisaurus* are featured by one lingual facet and a less prominent cingulum (as occur in SHN 540). These authors also noted that a primitive set of conditions might appear in some *Euhelopus* and *Camarasaurus*

teeth, depending of their position in the tooth row. Morphological variability of the lingual facets was also noted by Barret and Wang (2007). Suteethorn et al. (2013) also noted the presence of denticles in mamenchisaurid teeth. Denticles are present along tooth row in *Omeisaurus*, and *Mamenchisaurus* (e.g. He et al., 1988; Russell and Zheng, 1993; Upchurch and Barrett, 2000). Denticles are generally absent in macronarian sauropods with spatulate-shaped teeth such as *Euhelopus*, *Camarasaurus* and *Yongjinglong* (e.g. Osborn and Mook, 1921; Wilson and Upchurch, 2009; Li et al., 2014) being present only in distalmost teeth (Wilson and Sereno, 1998). The described spatulate-shaped teeth lacks denticles.

In conclusion, the presence of a spatulate-shape morphology, with more than one lingual facet (and sometimes a medial ridge) and the absence of denticles is a combination more derived than the condition present in Mamenchisauridae, and it is only present in the macronarians *Euhelopus*, *Camarasaurus* and *Yongjinglong*. This combination is shared by the Portuguese Upper Jurassic spatulate-shaped teeth, and they are tentatively attributed to Macronaria.

Indeed, it is difficult to split the tooth morphology of *Euhelopus* (a somphospondylian form) from *Camarasaurus* (a camarasaurid), because of the overlapping of their morphological variability (Marsh, 1878; Osborn and Mock, 1921; Wiman, 1929; Ostrom and McIntosh, 1966; McIntosh et al., 1996; Wilson and Upchurch, 2009; Suteethorn et al., 2013), including some differences noted by other authors (Barret and Wang, 2007, Sánchez-Hernandez et al., 2007; Wilson and Upchurch, 2009). The SI values of *Euhelopus* and *Camarasaurus* are similar (Sánchez-Hernández, 2007; Wilson and Upchurch, 2009), although Chure et al. (2010) obtained higher values values for *Euhelopus* (2.20-3.33, average=2.50) than *Camarasaurus* (1.57-2.47, average=1.92). If Chure et al. (2010) is correct, the Portuguese sample fall into the range of *Camarasaurus*. The presence of circular bosses in *Euhelopus* differentiates it from *Camarasaurus* (Wilson and Upchurch, 2009). Nevertheless, one tooth (SHN 541) of our sample presents this type of structure associated to the ridge-like border of the lingual facet.

According to the known sauropod paleobiodiversity for the Iberian Upper Jurassic, which includes the presence of basal macronarians such as the camarasaurid *Lourinhasaurus alenquerensis* (Mocho et al., 2013a,b, 2014a), it is more reasonable to accept that these teeth belong to a taxon more related to *Camarasaurus* than to *Euhelopus*. *Euhelopus* is related to Euhelopodidae, an exclusive group of the Lower Cretaceous of Asia (D'Emic, 2012; D'Emic et al., 2013). Nevertheless, new material is needed in order to improve the taxonomic assignation proposed herein.

6.5.3. Compressed cone-chisel-shaped teeth

Several compressed cone chisel-shaped teeth from the Portuguese Upper Jurassic are described in this section. They show high morphological variability and three main morphotypes are discriminated: *i*) morphotype I, with an intermediate morphology between spatulate-shaped teeth (e.g. *Camarasaurus* or *Euhelopus*) and compressed cone-chisel-shaped teeth, *ii*) compressed cone-chisel-shaped teeth with expansion of the apex and cylindrical base, and *iii*) compressed cone-chisel-shaped teeth without marked expansion of the apex. The presence of a lower SI, non-oval apical wear facets on the labial or lingual face, and the presence of carinae are features used herein to distinguish these teeth from the pencil-shaped morphotype. In teeth lacking the apex, the attribution to the compressed cone-chisel-shaped or to the pencil-shaped morphology is difficult to establish.

Morphotype I

Material: Ten teeth are assigned to the morphotype I: SHN 542-547, 550-552, 554, 556, 559, 572 and MG8772.


a.I
b.I
0.5cm
awf
a.II
a.III
a.IV
a.V
b.II
b.III
b.IV
b.V
rudimentary lf
c.I
d.I
cwf
"v"wf
c.II
c.III
c.IV
c.V
d.II
d.III
d.IV
d.V
lag
cwf
bwf
e.I
e.II
e.III
e.IV
f.I
f.II
f.III
f.IV
h.I
i.I
g.I
awf
lb
h.II
h.III
i.II
i.III
i.IV
i.V
j.I
awf
g.II
g.III
h.IV
h.V
j.II
j.III
j.IV
j.V

Locality and horizon: These teeth were found in several localities on Caldas da Rainha, Peniche and Lourinhã municipalities (see S.4) being present in Alcobaça, Praia de Amoreira-Porto Novo, Sobral, and Bombarral Formations, and resulting in a stratigraphic range from middle/upper Kimmeridgian to Tithonian (Fig. 6.2; Manuppella et al., 1999; Kullberg et al., 2006; Schneider et al., 2009; Azerêdo et al., 2010).

Description: These teeth present a general intermediate morphology between the spatulate-shaped morphotype typical for *Camarasaurus* (e.g. Gilmore, 1925; Ostrom and McIntosh, 1966; Madsen et al., 1995), *Euhelopus* (Wilson and Upchurch, 2009; Poropat et al., 2013) or *Mamenchisaurus* (Ouyang and Ye, 2002) and the compressed cone-chisel-shaped morphology (following Calvo, 1994) common in some titanosauriforms (Upchurch et al., 2004; Chure et al., 2010). The teeth belonging to the morphotype I are generally bigger (with the exception of SHN 572) than morphotype II and III. The crown has a slight expanded apex supported by a peduncle. The peduncle is slightly labiolingually compressed in cross-section with an elliptical to D-shaped outline. The labiolingual compression becomes more pronounced in the apex, which bears a lenticular cross-section. The apex is distally deflected as occur in heart- and spatulate-shaped tooth (Fig. 6.9) and bears a slight torsion relatively to the tooth axis (twisted axially through an arc of 30-45°, Fig. 6.9b.I, c.I, h.I, i.I, k.I). The crown are generally straight (e.g. Fig. 6.9e, SHN 546; Fig. 6.9f, SHN 547) and bears a slightly mesial imbrication. Furthermore, in some cases the crown can bear general sigmoidal curvature in labial/lingual view, as occur in SHN 543 (e.g. Fig. 6.9b). In these morphotype, the apex is particularly large (around a half of the total height of the crown). The transition between the base of the crown and the apex in the mesial edge is pronounced resulting in a shoulder. Taking into account the variability present in *Abydosaurus* (Chure et al., 2010) or *Giraffatitan* (Janensch, 1936), the distal deflection of the apex and the degree of imbrication is related with the position in the tooth row. The SI of the present sample ranges between 2.7-3.3.

In the apex, labial and lingual sides are apicobasally convex and flat-to-concave, respectively. When the carinae is present, it is more developed in the mesial edge than in the distal one. Nevertheless, the distal one is generally longer. In the preserved teeth, there is not a complex cingulum on the lingual face of the peduncle (no well-developed lingual facets are visible). Denticles on the apex are also absent.

On the labial face, it is possible to identify an apicobasal bulge bordered by two smooth apicobasal grooves. The distal groove bordering the apicobasal bulge is generally deeper than the mesial one (only present in the teeth with a less pronounced distal deflection of the apex) (Fig. 6.9f, SHN 547). These labial grooves do not extend up to the base of the crown, and they are longer in the teeth with more pronounced medial imbrication (Fig. 6.9b, SHN 543). The labial bulge is inflated at the apex as occurs in spatulate-shaped teeth such as in *Camarasaurus* or in the Portuguese Upper Jurassic specimens.

Figure 6.9. Compressed cone-chisel-shaped teeth from the Upper Jurassic of the Lusitanian Basin, morphotype I. SHN 550 (Peralta) in apical (a.I), lingual (a.II), labial (a.III), distal (a.IV) and mesial (a.V) views. SHN 543 (Baleal) in apical (b.I), lingual (b.II), labial (b.III) distal (b.IV) and mesial (b.V) views. SHN 551 (Peralta) in apical (c.I), lingual (c.II), labial (c.III), distal (c.IV) and mesial (c.V) views. SHN 541 (Porto Dinheiro) in apical (d.I), lingual (d.II), labial (d.III), distal (d.IV) and mesial (d.V) views. SHN 546 (Vermelha) in lingual (e.I), labial (e.II), distal (e.III) and mesial (e.IV) views. SHN 547 (Pedras Muitas) in lingual (f.I), labial (f.II), distal (f.III) and mesial (f.IV) views. SHN 554 (Almagreira) in apical (g.I), labial (g.II) and distal (g.III) views. SHN 572 (Porto Dinheiro) in apical (h.I), lingual (h.II), labial (h.III), distal (h.IV) and mesial (h.V) views. SHN 544 (Peralta) in apical (i.I), labial (i.II), lingual (i.III), mesial (i.IV) and distal (i.V) views. SHN 545 (Peralta) in apical (j.I), lingual (j.II), labial (j.III), distal (j.IV) and mesial (j.V) views. Scale bar: 10mm.

The lingual face of the base of the crown is generally flat and bears a smooth apicobasal lingual crest, mesially bordered by a smooth groove (e.g. Fig. 6.9j, SHN 545). This crest is restricted to the apex of the crown.

Texture: All teeth show a wrinkled texture composed by apicobasal ridges connected by secondary ridges, resulting from the branching of the main ridges (Fig. 6.10). In some points, the connection between ridges becomes anastomosed. The ridges are more defined than in the heart- and spatulate-shaped teeth, and the branching is not so common. In the peduncle, ridges are longer and reach the apex (Fig. 6.10f). In the apex, these ridges become less pronounced (Fig. 6.10g, n) and in some cases, the surface is cut by the abrasion (Fig. 6.10b). No important features are observed next to the edges of the apex, probably because the presence of some wear (e.g. Fig. 6.10h).

Figure 6.10. Wrinkling pattern on compressed cone-chisel-shaped teeth (morphotype I) from the Upper Jurassic of the Lusitanian Basin. The position of each photo is indicated on d (SHN 545), e (SHN 543) and L (SHN 547). a-c, f, g: wrinkling pattern of SHN 543 (Baleal); h, m: wrinkling pattern of SHN 545 (Peralta). i-k: wrinkling pattern of SHN 547 (Pedras Muitas). Black scale bar: 10mm; white scale bar: 1mm. bi – ridge bifurcation; de – ridge/scale deflection; ri – ridge.

On the transition with the root, the wrinkling pattern is smooth and the ridges are less deep. On the carinae is also possible to observe a deflection of the ridges (Fig. 6.10h), and here, they are shorter and acquired a scale-like morphology. In SHN 543, on the lingual side of the peduncle, close to the medial and lingual edge, the ridges assume a scale-like morphology. This scale structures are longer than in the heart- and spatulate-shaped teeth (Fig. 6.10a). Herein, the ridges are concentrated and diverge in a similar way as occur in the lingual facets of the spatulate-shaped teeth (see spatulate-shaped teeth description) (Fig. 6.10a). Although the presence of these agglomerations, they do not form a true lingual facet.

Wear pattern: The wear pattern present in this morphotype is distinct to the wear pattern observed in the heart- and spatulate-shaped teeth described above. In the less worn teeth, the apex generally present an apical wear facet (Fig. 6.9b, SHN 543, Fig. 6.9i, SHN 545; Fig. 6.9g, SHN 554) slightly mesial displaced. The apical facets are almost subhorizontal, but in more advanced stages, they acquired >30º of slope. The preserved apicomesial wear facets face lingually. In teeth with more advanced wear, the apicomesial wear facet becomes longer and progresses on the mesial edge of the apex (Fig. 6.9c; SHN 551, SHN559). On SHN 547 (Fig. 6.9f) and SHN 551 (Fig. 6.9c), the distal wear facet is present, and, in a more advanced stage of wear (Fig. 6.9c, SHN 551), the distal wear facet is more pronounced than the mesial one, suggesting that during the wear process, the distal wear becomes steeper than the mesial one. The initial lingual slope of the apical, distal and mesial facets disappears along the wear. SHN 542 is strongly worn out and a V-shaped wear facet is present, with a longer distal wear facet (Fig. 6.9d).

Morphotype II

Material: Five teeth and fragments are assigned to the morphotype II: SHN 549, MG 8779, MG 27890-95.

Locality and horizon: These teeth were found in several localities in Leiria, Vila Nova de Ourém and Torres Vedras municipalities (see S.4) being present in Alcobaça and Sobral Formations, and resulting in a stratigraphic range spanning from the middle/upper Kimmeridgian to lower Tithonian (Fig. 6.2; Manuppella et al., 1999; Kullberg et al., 2006; Scheneider et al., 2009; Azerêdo et al., 2010).

Description: This morphotype shares some features with the morphotype I: similar SI values; the presence of peduncle; lingual crest; and labial bulge. These teeth present a general compressed cone-chisel-shaped morphology (following Calvo, 1994) and the crown is formed by a marked expanded apex supported by a peduncle constricted at the base (Fig. 6.11). An interesting aspect of this morphotype is the fact that the preserved teeth described herein are significantly smaller than the teeth assigned to the morphotype I. The biggest tooth of the sample is MG 8779 from Ourém (Fig. 6.11a).

Unlike morphotype I, the peduncle is circular in cross-section becoming compressed labiolingually up to apex. At mid-height of the crown, the peduncle expands mesiodistally, giving place to an expanded apex. Carinae start to differentiate when the apex starts to expand. In the apex, the labial and lingual faces are transversely convex and convex-to-flat, respectively. In some teeth, the apex bears a distal deflection (MG 125 and MG 27894), and is generally slightly twisted axially through an arc of no more than 20º (Fig. 6.11a.I, b.I). The lingual face of the peduncle does not bear a complex cingulum with lingual facets. On the lingual side, an apicobasal crest is observed, bordered by two lateral smooth apicobasal grooves, becoming smoother toward the base (Fig. 6.11b.IV, c.III, d.III). These crests and grooves are more marked than in morphotype I. These grooves could be limited by carinae, which bear a slight lingual deflection (e.g. MG 27891). The labial side bears an apicobasal bulge displaced to the medial edge and bordered by two labial grooves, the distal one more marked as occur in the morphotype I. Similar to the morphotype I, the labial mesial groove is smooth and almost absent. In mesial view, the apex bears a general lingual curvature (e.g. Fig. 6.11b.III) up to its distal tip.

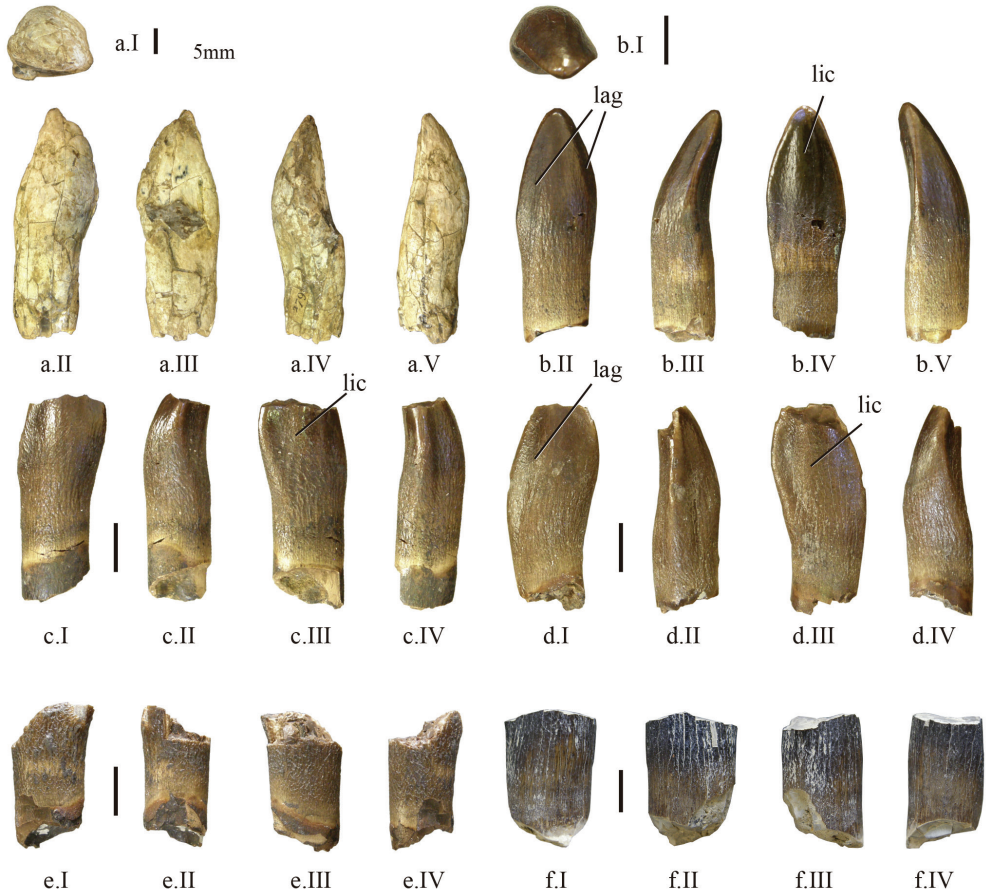


Figure 6.11. Compressed cone-chisel-shaped teeth from the Upper Jurassic of the Lusitanian Basin, morphotype II. MG 8779 (Ourém) in apical (a.I), labial (a.II), lingual (a.III), distal (a.IV) and mesial (a.V) views. MG 27891 (Guimarota) in apical (b.I), labial (b.II), mesial (b.III) lingual (b.IV) and distal (b.V) views. MG 27892 (Guimarota) in labial (c.I), mesial (c.II), lingual (c.III) and distal (c.IV) views. MG 27894 (Guimarota) in labial (d.I), distal (d.II), lingual (d.III) and mesial (d.IV) views. MG 27895 (Guimarota) in labial (e.I), mesial (e.II), lingual (e.III) and distal (e.IV) views. SHN 549 (Praia Azul) in labial (f.I), lingual (f.II), distal (f.III) and mesial (f.IV) views. Scale bar: 5mm.

Texture: All teeth show a wrinkled texture (except in MG 8779 where the enamel is not well-preserved) similar to the first morphotype (Fig. 6.12). The wrinkling pattern is composed by apicobasal ridges connected by secondary ridges, which results from the bifurcation of the main ridges (Fig. 6.12h). The ridges are similar in morphology to those of the morphotype I, and not so well-defined than in the morphotype III. The degree of branching on these ridges is not so pronounced than in the spatulate-shaped teeth (Fig. 6.8). In the apex, these ridges become smoother but there are no important signs of wear in the available teeth. Close to carinae, these ridges deflected and become oblique. This deflection only appears when the carinae start to individualize. In the base of the peduncle, no deflection is observed. The ridges only diverge slightly from the mesial and distal borders of the peduncle near carinae (Fig. 6.12i). In the transition between crown and root, the wrinkling pattern becomes smoother.

Wear pattern: MG 8779 and Guimarota teeth do not show any sign of wear, becoming impossible to obtain a wear pattern for this morphotype.

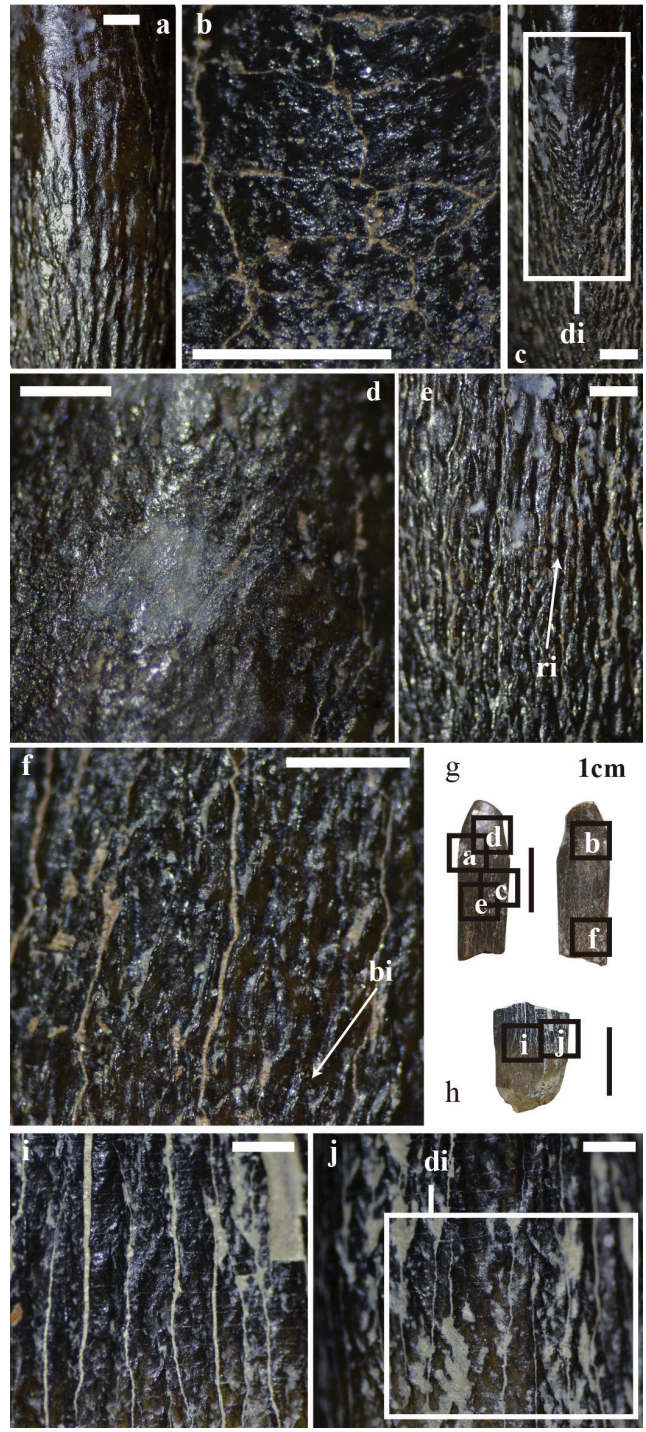


Figure 6.12. Wrinkling pattern on compressed cone-chisel-shaped teeth (morphotype II and morphotype III) from the Upper Jurassic of the Lusitanian Basin. The position of each photo is indicated on g (SHN 548) and h (SHN 549. a-f: wrinkling pattern of SHN 548 (Valmitão, morphotype III); i, j: wrinkling pattern of SHN 549 (Praia Azul, morphotype II). Black scale bar: 10mm; white scale bar: 1mm. bi – ridge bifurcation; de – ridge/scale deflection; ri – ridge.


a.I
awf
b.I
awf
0.5cm
awf
cwf
a.II
a.III
a.IV
a.V
b.II
bIII
b.IV
b.V
c.I
awf
d.I
awf
awf
c.II
c.III
c.IV
c.V
d.II
d.III
d.IV
d.V
e.I
e.II
e.III
e.IV
f.I
f.II
f.III
f.IV
g.I
g.II
g.III
g.IV
g.V
h.I
h.II
h.III
h.IV

Morphotype III

Material: Ten teeth are assigned to the morphotype III: SHN 573-81, and SHN 548 with doubt.

Locality and horizon: Several localities of Caldas da Rainha, Lourinhã and Torres Vedras municipalities (see S.4) involving outcrops of the Alcobaça, Praia de Amoreira-Porto Novo, Sobral, Freixial Formations, and with a stratigraphic range spanning from middle/upper Kimmeridgian to Tithonian (Fig. 6.2; Manuppella et al., 1999; Kullberg et al., 2006; Scheneider et al., 2009; Azerêdo et al., 2010).

Description: This type of teeth has an intermediate morphology between compressed cone-chisel teeth and pencil-shaped teeth, which feature most derived titanosaurs and diplodocoids (e.g. Calvo, 1994; Upchurch and Barrett, 2000; Wilson, 2005; Cerda and García, 2010; Chure et al., 2010; Díez-Díaz et al., 2012a, 2014; D'Emic et al., 2013; Fig. 6.13). Nevertheless, several features are used herein to consider them as compressed cone-chisel-shaped teeth: low SI, the presence of carinae, slight expansion of the apex, and the absence of oval apical wear facets (see discussion below).

The crowns are generally long and straight and, in some cases, with a slight distally deflected apex (e.g. Fig. 6.13a, SHN 577; Fig. 6.13c, SHN 578). Furthermore, in some cases, the crown can bear a slight "S"-shaped curvature, as occurs in SHN 578 (Fig. 6.13c). The apex is slightly expanded (Fig. 6.13c, SHN 578; Fig. 6.13d, SHN 580), less than in the morphotype II (Fig. 6.11). According with the total crown height, the peduncle is higher than in previous morphotypes. The peduncle bears a circular cross-section assuming a D-shaped cross-section in the transition with the apex. The apex is shorter than in the morphotypes I and II. SHN 576 bears an elliptical cross-section. Generally, the apex on this morphotype is labiolingually compressed. In some teeth, the apex twisted axially through an arc of approximately 30º (e.g. Fig. 6.13a.I, SHN 577; Fig. 6.13c.I, SHN 578). The SI of the sample ranges between 2.6 and 3.4. In mesial/distal view, teeth bear a straight peduncle and the crown deflects lingually at the apex.

The lingual face is convex apicobasally in the peduncle and becomes progressively flat toward the apex. No apicobasal lingual crest or labial bulge are present in these teeth, differentiating them from those of the morphotypes I and II. SHN 548 presents a very slight expansion of the apex and the crown presents a smooth apicobasal groove on the lingual surface of the apex close to the mesial edge (Fig. 6.13b). The apex also develops well-defined mesial and distal carinae. These features are similar to those present in teeth of the morphotype II. However, SHN 548 presents a longer peduncle. The SHN 548 ornamentation (Fig. 6.12a-f) is more similar with the texture present in other morphotype III (Fig. 6.14) teeth than in morphotype II teeth (Fig. 6.12h-i). For the moment, SHN 548 is assigned with doubt to the morphotype III.

Texture: All teeth show a wrinkled texture. The wrinkling pattern is composed by apicobasal ridges connected by secondary ridges, which results from the branching of the main ridges, as occur in previous described morphotypes. Nevertheless, in this morphotype, these apicobasal ridges are

Figure 6.13. Compressed cone-chisel-shaped teeth from the Upper Jurassic of the Lusitanian Basin, morphotype III. SHN 577 (Valmitão) in apical (a.I), lingual (a.II), labial (a.III), mesial (a.IV) and distal (a.V) views. SHN 548 (Valmitão) in apical (b.I), lingual (b.II), labial (b.III) distal (b.IV) and mesial (b.V) views. SHN 578 (Valmitão) in apical (c.I), lingual (c.II), labial (c.III), mesial (c.IV) and distal (c.V) views. SHN 580 (Assenta) in apical (d.I), lingual (d.II), labial (d.III), distal (d.IV) and mesial (d.V) views. SHN 575 (Valmitão) in lingual (e.I), labial (e.II), mesial (e.III) and distal (e.IV) views. SHN 579 (Peralta) in labial (f.I), lingual (f.II), distal (f.III) and mesial (f.IV) views. SHN 574 (Valmitão) in apical (g.I), lingual (g.II) labial (g.III), mesial (g.IV) and distal (g.V) views. SHN 573 (Vale de Pombas) in lingual (h.I), labial (h.II), mesial (h.III) and distal (h.IV) views. Scale bar: 5mm.

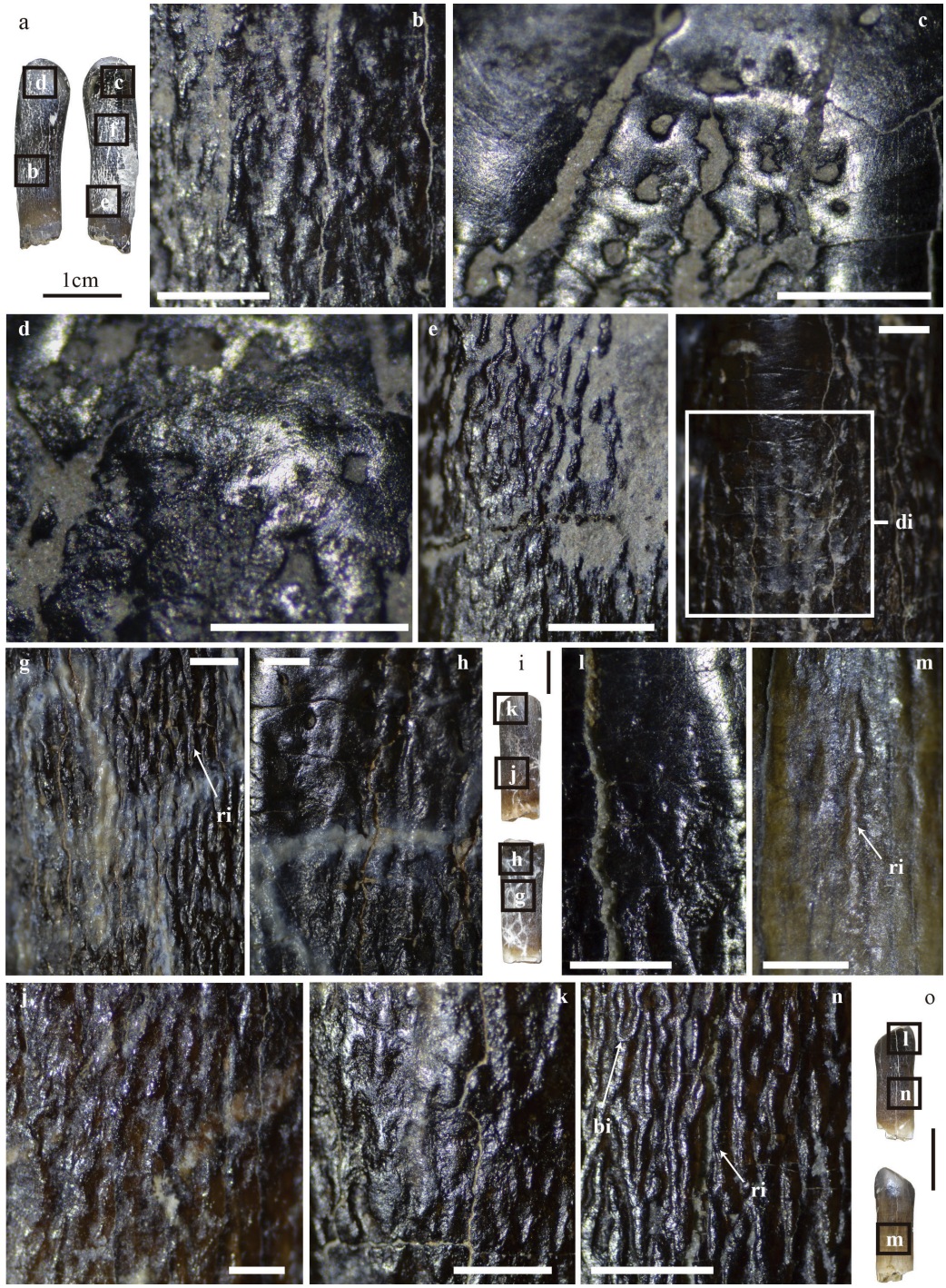


Figure 6.14. Wrinkling pattern on compressed cone-chisel-shaped teeth (morphotype III) from the Upper Jurassic of the Lusitanian Basin. The position of each photo is indicated on a (SHN 578), i (SHN 575) and o (SHN 580). b-f: wrinkling pattern of SHN 578 (Valmitão). g, h, j, k: wrinkling pattern of SHN 575 (Valmitão). l, m, n: wrinkling pattern of SHN 580 (Assenta) Black scale bar: 10mm; white scale bar: 1mm. bi – ridge bifurcation; di – ridge divergence on the base of the carinae; ri – ridge.

more well-defined and show a less degree of bifurcation (Fig. 6.14b, g, n) than in morphotype I and spatulate-shaped teeth. In the apex, the wrinkling pattern becomes smoother and not so individualized. On the teeth with more pronounce wear, lingual and labial surfaces are truncated by abrasion, resulting in the removal of the enamel ornamentation (Fig. 6.14c, l). The ornamentation of the labial surface of the SHN 580 peduncle is particularly unusual, showing the presence of well-spaced apicobasal ridges (Fig. 6.14m). As occur in the previous morphotype, close to the transition between the crown and the root, the wrinkling pattern becomes smoother. In this morphotype, the apex is restricted to a more apical position, and, at this point, the wrinkling pattern is generally softly (Fig. 6.14d). The ridges diverge slightly from the mesial and distal borders of the peduncle and the apex (Fig. 6.14f).

Wear pattern: The wear pattern seems to be similar to the pattern observed in the compressed cone-chisel-shaped teeth assigned to the morphotype I. Nevertheless, the sample is too small and most of the preserved teeth are incomplete to achieve a clear sequence of wear. Teeth with an incipient wear bear an apical wear facet on the mesial edge of the apex (Fig. 6.13c, SHN 578). The SHN 580 (Fig. 6.13d) presents an appreciable wear, but only bears an apical wear facet slopping mesially or distally (the orientation of this tooth is not clear). SHN 548 (Fig. 6.13b) presents an advanced stage of wear bearing a subhorizontal apical wear facet associated to a distal wear facet with high inclination relatively to the basal plan. Nevertheless, some doubts exist in the assignation of this tooth to the morphotype II.

Discussion: A compressed cone-chisel-shaped morphology as in the morphotype I and II was assigned to Titanosauriformes and featured by the presence of labial and lingual grooves and crests, high SI values (not so higher than in pencil-shaped teeth) and apex slightly expanded mesiodistally (Upchurch et al., 2004; Chure et al., 2010). No infra-generic determination is possible due the absence of diagnostic features, a relative common situation for sauropod teeth (Canudo et al., 2002, García and Cerda, 2010). Upchurch et al. (2004) noted that this type of morphology is a "mosaic of features" between the spatulate-shaped teeth common in macronarians (e.g. Gilmore, 1925) and titanosaurian/diplodocid teeth (e.g. Cerda and García, 2010) and assign it as characteristic of basal titanosauriforms.

The studied teeth share their overall morphology with some basal titanosauriforms such as *Abydosaurus* (Chure et al., 2010), *Ligabuesaurus* (Bonaparte et al., 2006), *Giraffatitan* (Janensch, 1936), *Europasaurus* (Marpmann et al., 2015), *Sauroposeidon* (Rose, 2007; D'Emic and Foreman, 2012) or *Astrophocaudia* (D'Emic, 2013), and they are congruent with the stratigraphic range of this group of sauropods (D'Emic, 2012; Mannion et al., 2013). This morphotype is relatively common in Upper Jurassic to Lower Cretaceous sediments (e.g. Sauvage, 1987-88; Janensch, 1936; Lapparent, 1943; Rauhut, 2000; Ruiz-Omeñaca and Canudo, 2005; Bonaparte et al., 2006; Chure et al., 2010; Saegusa and Tomida, 2011; D'Emic, 2013). Recent phylogenetic hypotheses suggest the presence of this tooth morphology in basal members of Somphospondyli such as in *Astrophocaudia* and *Sauroposeidon* (D'Emic and Foreman, 2012; D'Emic, 2013). Otherwise, derived titanosaurs acquired pencil-shaped teeth (convergent with diplodocoids, Wilson and Sereno, 1998; Upchurch et al., 2004) differing significantly from the tooth morphology present in basal titanosauriforms. Firstly, titanosaurs have longer teeth (see SI values, Chure et al., 2010) and do not bear an expanded apex with well-developed carinae as in basal titanosauriforms (e.g. Janensch, 1936; Chure et al., 2010; D'Emic and Foreman, 2012). The development of labial and lingual crests (and respective grooves) in titanosauriforms is generally absent in titanosaur pencil-shaped teeth (e.g. Upchurch et al., 2004; Wilson, 2005; Cerda and García, 2010; Díez-Díaz et al., 2012a).

The teeth assigned herein to the compressed cone-chisel-shaped morphology bear some variability mainly related to the degree of deflection of the apex, the morphology of the labial face (presence of absence of grooves/crests), the peduncle height, and the expansion of the apex. This type of variability is fairly common in titanosauriforms with a well preserved tooth row such

Abydosaurus or *Giraffatitan* suggesting that the variability is probably related with the position of each tooth in the tooth row. Furthermore, possible ontogenetic variability have been also noted by some authors (e.g. Cerda and García, 2011; Holwerda et al., 2015) fact that might be related with a switch of the diet between juvenile and adult individuals (Fiorillo, 1991, 1998; Carballido and Pol, 2010; Whitlock, 2011; Díez-Díaz et al., 2012a). *Giraffatitan* bears an appreciable variability along the tooth row presenting higher, robust and spatulate-like teeth mesially located, and more slender teeth with constricted crown base and expanded apex distally located. "*Bothriospondylus*" remains from the Upper Jurassic of Damparis (France, Lapparent, 1943) also present an important morphological variability.

The morphotype I is particularly similar to most of the teeth of *Giraffatitan*, which bears an intermediate morphology between spatulate-shaped (e.g. *Camarasaurus*, Ostrom and McIntosh, 1966) and compressed cone-chisel-shaped teeth (e.g. *Sauroposeidon*, Rose, 2007, D'Emic and Foreman, 2012), including the presence of rudimentary lingual facets. As in *Giraffatitan*, the teeth of morphotype I generally present an appreciable size when compared with teeth of morphotype II and III. In the figured teeth of *Giraffatitan* (Janensch, 1936), smaller teeth generally present a more stylized morphology as occur in Guimarota teeth assigned to morphotype II, also bearing a small size when compared with those of the morphotype I. This suggests for the possibility of some ontogenetic variability. As it was referred above, tooth with morphological disparity along the ontogeny have been reported and suggested by several authors (Chiappe et al., 2001, 2005; García and Cerda, 2010; Whitlock et al., 2010; Díez-Díaz et al., 2012a, b, 2014; Holwerda et al., 2015). Holwerda et al. (2015) noted that in possible *Camarasaurus* embryonic teeth (Britt and Naylor, 1994) are more slender than the teeth of subadult and adult individuals (Gilmore, 1925; Madsen et al., 1995; Fiorillo, 1998; McIntosh et al 1996a, b).

The distal teeth of *Giraffatitan* generally bear more slender morphology with restricted peduncles similar to those of the morphotype II identified herein (HMN MB.R.2181.1-3, 2390; Janensch, 1936). So, the morphological spectrum between morphotype I and II also might be explained by positional variability along the tooth row. The teeth assigned to morphotype II are generally smaller. Nevertheless, this morphology is also well-developed in Damparis sauropod from the French Upper Jurassic record (see Lapparent, 1943), which bears an appreciable size. This suggests slender morphotype might reach sizes comparable to the sizes observed in morphotype I of the studied Portuguese sample and in *Giraffatitan* teeth.

The teeth assigned to morphotype III present a very slight expansion of the apex with a longer peduncle than the teeth assigned to the morphotypes I and II. This type morphology presents some shared features with pencil-shaped teeth, which characterize the most derived titanosauriforms and diplodocoids (Calvo,1994; Upchurch and Barrett, 2000; Upchurch et al., 2004; Wilson, 2005; Cerda and García, 2010; Díez-Díaz et al., 2012a, 2014; D'Emic et al., 2013), such as the presence of parallel mesial and distal edges, subcircular cross-section at the base and no lingual concavity. Nevertheless, lower SI values, the presence of carinae with markedly compressed apex and the absence of oval wear facets on the labial/lingual face relates these teeth with the compressed cone-chisel morphology. Some derived titanosaurs can present non-oval apical and v-shaped wear facets (*Nemegtosaurus*, Calvo, 1994; Wilson, 2005). The morphotype III teeth are generally smaller. Some teeth assigned to *Giraffatitan* share some similarities with this morphotype. *Abydosaurus* presents a morphological variability that comprises teeth assigned to the morphotype II and teeth with no mesiodistal expansion of the apex and higher peduncles, as occur in the morphotype III (Chure et al., 2010, fig. 4d, e). So, the observed differences between morphotype II and III can be explained by the presence of morphological variability along the tooth row, fact well supported by the common positional variability in sauropods with spoon-, spatulate- and compressed cone-chisel-shaped teeth such as *Turiasaurus* (Royo-Torres et al., 2006; Royo-Torres and Upchurch, 2012), *Spinophorosaurus* (Remes et al., 2009; pers. observ., PM), *Patagosaurus* (Bonaparte, 1986; Holwerda et al., 2015),

Mamenchisaurus (Ouyang and Ye, 2002), *Omeisaurus* (He et al., 1988), *Camarasaurus* (Gilmore, 1925; Ostrom and McIntosh, 1966; McIntosh et al., 1996a, b), *Abydosaurus* (Chure et al., 2010), *Giraffatitan* (Janensch, 1936), *Euhelopus* (Wiman, 1929; Wilson and Upchurch, 2009), and the Damparis sauropod, a putative titanosauriform (Lapparent, 1943; Mannion, 2010).

In conclusion, the three morphotypes attributed to a compressed cone-chisel-shaped morphology might pertain to the same taxonomic unit: morphotype I representing an advanced ontogenetic stage relatively to the morphotype II and III that are generally smaller. Nevertheless, teeth of the morphotype I and II are present in the same ontogenetic stage in *Giraffatitan*. The differences between morphotype II and III might be explained by different positions on the tooth row. It is not possible to test if they represent different taxonomic units, and so, the hypothesis that the observed morphological disparity has a taxonomic origin is not ruled out.

D'Emic (2012) proposed the presence of maxillary teeth twisted axially through an arc of 30–45° as synapomorphy of Brachiosauridae being present in the basal titanosauriforms *Giraffatitan*, *Abydosaurus*, and *Europasaurus*. Recent phylogenetic approaches suggested to place *Europasaurus* as a basal camarasaraumorph more derived than *Camarasaurus* (Carballido et al., 2011; Carballido and Sander, 2014; Li et al., 2014 following Carballido and Sander, 2014 data matrix; Royo-Torres et al., 2014a) against the brachiosaurid hypothesis (D'Emic, 2012; Mannion et al., 2013; Li et al., 2014 following D'Emic, 2012 and Mannion et al., 2013 data matrices). If *Europasaurus* corresponds to a non-brachiosaurid basal macronarian, this feature might be a synampomorphy of a more inclusive group within Camarasauromorpha, or a convergence with brachiosaurids. The compressed cone-chisel-shaped teeth from the Upper Jurassic of the Lusitanian Basin described herein present different degrees on the apex rotation, but some of them twisted axially through an arc more than 45°, in particularly, on the teeth assigned to the morphotype I and III. This rotation is not so pronounced than in the teeth assigned to morphotype II but this might be related to the presence of a small sample for morphotype II.

The described morphotypes present some differences on the wrinkling pattern. On the morphotype I the ridges are not so well-marked and more spaced than in morphotype III, and the degree of bifurcation is bigger. Besides the small sample, the morphotype II seems to shares a similar wrinkling pattern with morphotype III. Some authors suggested that the wrinkling pattern might vary along the ontogeny. In particularly, isolated teeth collected in Laño fossil site were considered as pertaining to juvenile and adult individuals related to the titanosaur *Lirainosaurus* (Díez-Díaz et al., 2012a). Díez-Díaz et al. (2012a) described different wrinkling pattern between juveniles and adult specimens, being smother the juvenile condition. Holwerda et al. (2015) noted for small differences between embryonic material possible related with *Camarasaurus* and adult specimens of this taxon (and also in diplodocids), suggesting for the presence of minor ontogenetic variability relatively to the wrinkling pattern in non-titanosaur neosauropods. If, the studied teeth belonging to morphotype I and III corresponds to ontogenetic series of the same taxon, this suggest that in Titanosauriformes the ontogeny might conduct to some variability on the wrinkling pattern. Nevertheless, this hypothesis only will be confirmed with the discovery and description of teeth of more complete ontogenetic series assigned to the same taxonomic unit.

6.5.4. Pencil-shaped teeth

Material: Three teeth (MNHNUL/AND.302, 303, 304) from Andrés-site are described and related to the pencil-shaped morphology.

Locality and horizon: These teeth were reported from the Andrés fossil site in Santiago de Litém (Pombal) (see S.4), placed in the Bombarral Formation, Tithonian in age (Manuppella et al., 2000; Kullberg et al., 2006; Fig. 6.2).

Description: MNHNUL/AND.302 is composed by crown and part of the row (the transition between the crown and the row is smooth) (Fig. 6.15c). This tooth is one of the biggest pencil-shaped teeth recovered from Andrés quarry, and presents a general slight curvature, where the convexity faces labial. The base of the teeth is circular in cross-section but becomes labiolingually compressed next to the apex. Although they are convex, the lingual face is more flat transversely than the lingual face. The present tooth bears an apical oval wear facet on the lingual side, with a high inclination (more than 80º). The lingual wear facet might suggest a maxillary or premaxillary position. In labial view, next to apex, the tooth is slightly expanded mesiodistally.

The MNHNUL/AND.303 is a small pencil-like tooth, with a rudimentary apical wear facet lingually located (Fig. 6.15a). The tooth does not present a well-defined texture, probably due preservation. The tooth lacks a slight mesiodistal expansion as in MNHNUL/AND.302 and 304. The base of the tooth is circular in cross-section but becomes labiolingually compressed next to the apex. The lingual face is flatter than the labial face.

The MNHNUL/AND.304 is also a pencil-shaped teeth (Fig. 6.15c), and preserves the crown and part of the tooth row. The base of the tooth is circular in cross-section but becomes labiolingually compressed next to the apex. It presents an apical lingual wear facet, suggesting a maxillary/premaxillary origin. The crown bears a slight mesiodistally expansion. MNHNUL/AND.304 bears a general curvature where the convexity faces labial, resulting in the lingual deflection of the apex. These tooth has smooth lingual grooves close to the mesial and the distal edges of the crown.

The SI value range of the described pencil-shaped teeth of Andrés site is 2,6-4. Nevertheless all studied teeth present some significant wear.

Texture: In MNHNUL/AND.304 and 303, the wrinkled texture is present but is smooth in the base of the crown and absent in the apex. In MNHNUL/AND.302, a net of smooth anastomosed ridges composes the wrinkled texture. A detailed figuration for the wrinkling pattern was not possible to perform at the moment, and the full preparation of Andrés tooth specimens will be important in order to obtain a better characterization of the wrinkling pattern for this type of morphology.

Discussion: Pencil-shaped teeth, i.e. cylindrical to subcylindrical crowns, are present in all diplodocoids (e.g. Janensch, 1936; Calvo, 1994; Christiansen, 2000; Upchurch and Barrett, 2000; Upchurch et al., 2004), more labiolingually compressed in *Dicraeosaurus* (Janensch, 1936). Also more derived titanosauriforms present pencil-shaped teeth, which share several features with diplodocoid teeth such as the presence of high SI values and subcylindrical crowns (e.g. Wilson, 2005; Chure et al., 2010; Cerda and García, 2010; Díez-Díaz et al., 2012a, b; D'Emic et al., 2013) or the loss of labial grooves and the lingual concavity (Upchurch et al., 2004). This features are also absent in MNHNUL/AND 302, 303 and 304. The pencil-shaped teeth of derived titanosauriforms and diplodocoids are particularly difficult to differentiate.

Some differences have been reported within Diplodocoidea, and they might be used in order to differentiate pencil-shaped teeth from Diplodocidae, Dicraeosauridae and Rebbachisauridae (Janensch, 1936; Upchurch and Barrett, 2000; Sereno and Wilson, 2005; Torcida Fernández-Baldor et al., 2011). Andrés teeth present subparallel mesial and distal edges in labial/lingual views, a common feature in diplodocoid teeth. Diplodocids and dicraeosaurids also bear a lingual curvature, as occur in MNHNUL/AND 303 and 304. The studied teeth bear some labiolingual compression, situation also documented for *Diplodocus* (Chirstiansen, 2000) and *Dicraeosaurus* (Janensch, 1936).

Andrés teeth differ from rebbachisaurids *Nigersaurus* and *Demandasaurus* by the absence of an asymmetrical enamel distribution (Sereno and Wilson, 2005). Sereno and Wilson (2005) considered as diagnostic of *Nigersaurus* the presence of a crown with prominent mesial and distal ridges (resulting in a trapezoidal cross-section) that is absent in Andrés teeth. In MNHNUL/AND.304, distal and mesial

borders are slightly acute, but without well-develloped carinae as in the rebbachisaurid *Demandasaurus* (Torcida Fernández-Baldor et al., 2011). *Demandasaurus* also presents longitudinal crests on the enamel surface (Torcida Fernández-Baldor et al., 2011).

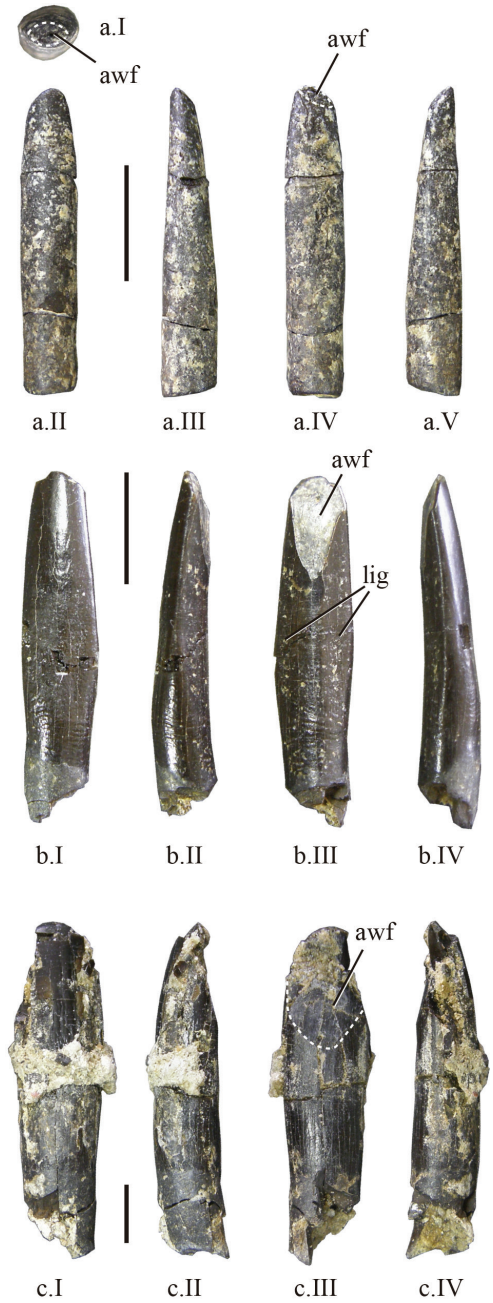


Figure 6.15. Pencil-shaped teeth from the Upper Jurassic of the Lusitanian Basin. MNHNUL/AND.303 (Andrés) in apical (a.I), lingual (a.II), mesial/distal? (a.III), labial (a.IV) and mesial/distal? (a.V) views. MNHNUL/AND.304 (Andrés) in labial (b.I), mesial/distal? (b.III), lingual (b.III) and mesial/distal (b.V) views. MNHNUL/AND.302 (Andrés) in labial (c.I), mesial/distal? (c.II), lingual (c.III) and mesial/distal? (c.IV) views. Scale bar: 5mm.

The SI value in Andrés teeth ranges from 2.6 to 4. Diplodocoids, titanosaurs, and the euhelopodids *Phuwiangosaurus* and *Huabeisaurus* acquired independently SI values higher than 4 (Upchurch et al., 2004; Chure et al., 2010; D'Emic et al., 2013). The presence of wear might explain the relatively small SI value for some of the Andrés specimens.

The presence of a well-defined oval apical wear facet on MNHNUL/AND 303, 304 is shared with diplodocids (Calvo, 1994; Upchurch and Barrett, 2000) but some variability in the position and angle is reported (Calvo, 1994; Christiansen, 2000). Nevertheless, Upchurch and Barrett (2000) suggested that the wear facets on diplodocids are labially located. Rebbachisaurids and *Dicraeosaurus* also present oval wear facets (Sereno and Wilson, 2005; Sereno et al., 2007) and in some *Dicraeosaurus* teeth, the apical wear facet could be developed on the edge of the apex (Janensch, 1936).

Wrinkling pattern on diplodocoids is poorly known. Holwerda et al. (2015) are noted the presence of asymmetrical enamel wrinkling distribution, as occur in MNHNUL/AND 302, 303 and 304. Nevertheless, a further detailed analysis is needed after the full preparation of the all specimens of Andrés quarry.

The presence of subcylindrical morphology, with a only slight labiolingually compression on the apex (more pronounced in MNHNUL/AND 304) without carinae, and the presence of an oval apical facet mainly located on the lingual side of the tooth allow relating, tentatively, these teeth to Diplodocoidea. According to the currently known Portuguese sauropod diversity during the Upper Jurassic (e.g. Bonaparte and Mateus, 1999; Mannion et al., 2012; Mocho et al., 2014b), and the absence of derived titanosaurs with pencil-shaped teeth with high SI values on the Upper Jurassic (e.g. Chure et al., 2010; D'Emic, 2012; D'Emic et al., 2013; Mannion et al., 2013) is reasonable to consider that these teeth might pertain to a diplodocoid form.

In the Upper Jurassic of the Iberian Peninsula, the record of pencil-shaped teeth is poor (Mannion et al., 2012). Martínez et al. (2000) provided one of the first references of a pencil-shaped tooth on the Iberian Upper Jurassic considering it as a diplodocoid tooth. Otherwise, also from Spain, in Villar del Arzobispo sediments (Tithonian-Early Berriasian) of the Carretera site, in Galve (Spain) was recovered a subcylindrical sauropod tooth, being suggested that this tooth might belong to a basal diplodocoid (Royo-Torres and Canudo, 2003; Canudo et al., 2005). Mannion et al. (2012) noted that this morphology is also present in more derived titanosaurs and considered both teeth as belonging to an indeterminate neosauropod pending further study. The most important references on the Iberian territory to this type of teeth come from Andrés quarry and some of them, briefly discussed herein. Malafaia et al. (2006, 2010) referred some of the pencil-shaped teeth from Andrés to Diplodocoidea, systematic approach supported by Mannion et al. (2012).

6.6. DISTRIBUTION ON SAUROPOD TOOTH MORPHOSPACE

Following Chure et al. (2010), in the figure 6.16 we plotted the average SI values presented by the several tooth morphologies identified for the Upper Jurassic of the Lusitanian Basin with other sauropodomorphs: *i*) heart-shaped teeth (including the three morphotypes defined by Mocho et al., 2012, in press), *ii*) spatulate-shaped teeth; *iii*) compressed cone-chisel-shaped teeth (including the three morphotypes defined herein); and *iv*) pencil-shaped teeth. In this analysis, the most worn teeth were removed.

The SI average in *Turiasaurus* teeth (1.25) and Portuguese heart-shaped teeth (1.40) is slightly different, probably due to the size of the sample (three teeth) for *Turiasaurus*, which is composed by teeth with a morphology close to those of the morphotype II defined by Mocho et al. (2012, in press). Nevertheless, the SI average of *Turiasaurus* (a sauropod with heart-shaped

teeth) fits in the range of the Portuguese Upper Jurassic heart-shaped teeth. The SI range of Portuguese Upper Jurassic heart-shaped teeth place them within the non-neosauropod sauropods morphospace (Figure 6.16) as well as, *Turiasaurus* teeth. This type morphology is so far only associated with non-dental material of basal eusauropods, in particularly, turiasaurs (Royo-Torres et al., 2006, 2009; Royo-Torres and Upchurch, 2012; Mateus et al., 2014). This allowed Mocho et al. (2012, in press) to suggest the tentative attribution of the Portuguese heart-shaped teeth to this clade. The presence of SI values close to 1 places the morphotype III outside the morphospace occupied by the non-neosauropod sauropods.

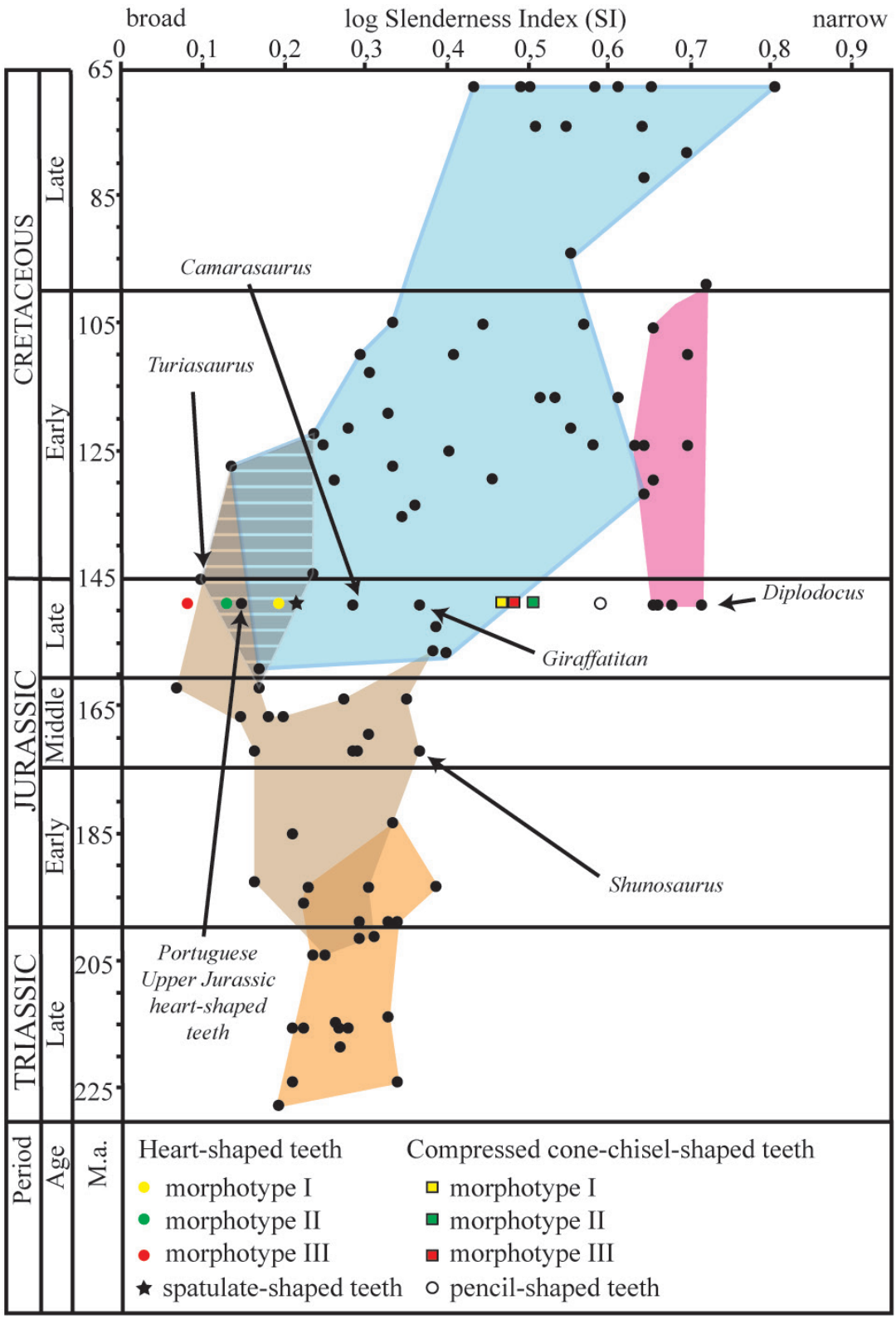
The spatulate-shaped teeth identified in the Portuguese Upper Jurassic, common in basal eusauropods and basal macronarians and herein tentatively attributed to Macronaria, fits within the morphospace obtain by Chure et al. (2010) for macronarian sauropods. The SI average for the Portuguese specimens is relatively low when compared with other macronarians with this type of morphology such as *Euhelopus* (e.g. Wiman, 1929) and *Camarasaurus* (e.g. Gilmore, 1925). Nevertheless, the sample is relatively small when compared with the numerous teeth assigned to *Camarasaurus* (e.g. Marsh, 1878; Gilmore, 1925; Ostrom and McIntosh, 1966; Madsen et al., 1995; McIntosh et al., 1996a, b).

Several specimens from the Portuguese Upper Jurassic record were related to the compressed cone-chisel-shaped teeth morphology common in basal Titanosauriformes (Upchurch et al., 2004). Nevertheless, only few specimens are totally complete and the sample might not be significant. The morphotype I, II and III described for the compressed cone-chisel-shaped teeth are placed in the morphospace occupied by macronarian sauropods (some fall outside of this morphospace due the presence of high SI values, in particular the morphotype III), with SI average of 2.97, 3.21 and 3.09, respectively. These values indicate that Portuguese Upper Jurassic compressed cone-chisel-shaped teeth are slender than in teeth of *Giraffatitan* (SI=2.33) or *Abydosaurus* (SI=2.79) and in Damparis sauropod (SI=2.46) (obtained by Chure et al., 2010). Nevertheless, several teeth of *Giraffatitan* and *Abydosaurus* present SI values higher than 3 (Janensch, 1936; Chure et al., 2010; pers observ., PM). A more complete sample of this type morphology from the Portuguese Upper Jurassic, *Giraffatitan*, *Abydosaurus* and *Europasaurus* is necessary to improve our knowledge about its morphological spectrum.

Finally, the two pencil-shaped teeth found in Andrés fossil site (MNHNUL/AND.303, 304) present SI values higher than basal titanosauriforms but smaller than diplodocids. Nevertheless, the SI values of Andrés specimens are closer to the morphospace occupied by diplodocoids (Chure et al., 2010), and the observed wear might explain these low values. On Chure et al. (2010) is possible to verify that some diplodocoid taxa present teeth with similar SI values with the Andrés specimens such as *Nigersaurus*, *Demandasaurus* or *Dicraeosaurus*. Future analyses, incorporating more specimens will be important do redefined the respective morphospaces presented by the diplodocoid clades.

6.7. TOOTH MORPHOLOGICAL VARIABILITY IN THE CONTEXT OF THE IBERIAN UPPER JURASSIC SAUROPOD FAUNAS

Four main tooth morphologies were identified for sauropods in the Portuguese Upper Jurassic record: heart-, spatulate-, compressed cone-chisel- and pencil-shaped teeth. The present sample suggests for the presence of a non-neosauropod eusauropod form, probably relate with Turiasauria (heart-shaped teeth, Fig. 6.3, previously suggested by Mocho et al., 2012, in press); a basal macronarian (spatulate-shaped teeth, Fig. 6.7); a basal titanosauriform (compressed cone-chisel-shaped teeth, Figs. 6.9, 6.11, 6.13) and diplodocoids (pencil-shaped teeth, Fig. 6.15). These is in accordance with the known paleobiodiversity for the Portuguese Upper Jurassic sauropod faunas, which includes turiasaurs (*Zby atlanticus*, Mateus et al., 2014), at least one diplodocid


broad
log Slenderness Index (SI)
narrow
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85
105
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145
165
185
205
225
CRETACEOUS
Late
Early
JURASSIC
Late
Middle
Early
TRIASSIC
Late
Camarasaurus
Turiasaurus
Diplodocus
Giraffatitan
Shunosaurus
Portuguese Upper Jurassic heart-shaped teeth
Period
Age
M.a.
Heart-shaped teeth
morphotype I
morphotype II
morphotype III
spatulate-shaped teeth
Compressed cone-chisel-shaped teeth
morphotype I
morphotype II
morphotype III
pencil-shaped teeth

(*Dinheirosaurus lourinhanensis*, Mannion et al., 2012), a camarasaurid basal macronarian (*Lourinhasaurus alenquerensis*, Mocho et al., 2014) and a basal macronarian probably related with Brachiosauridae (*Lusotitan atalaiensis*, Mannion et al., 2013). A heart-shaped tooth was found in association with the turiasaur *Zby atlanticus* holotype, supporting the assignation of this morphotype to Turiasauria clade.

Some tooth occurrences have been reported from the Spanish Upper Jurassic record. The heart-shaped morphotype was found in association with cranial and postcranial material, i.e. the teeth of *Turiasaurus riodevensis* (Royo-Torres et al., 2006; Royo-Torres and Upchurch, 2012). Another turiasaurian specimen with cranial and postcranial material was found in the Villar del Arzobisbo Formation at San Lorenzo (Teruel) bearing several associated heart-shaped teeth (Cobos et al., 2011). Canudo et al. (2010) refer to cf. *Turiasaurus riodevensis* a fragment of a dentary with some heart-shaped teeth from the Kimmeridgian of Asturias (Spain).

From the Upper Jurassic-basal Lower Cretaceous sediments of Spain, some teeth occurrences have been reported to the pencil-shaped morphology, one tooth (MUJA-0323) from the Lastres Formation at Villaviciosa, Asturias (Martínez et al., 2000), and another tooth from Carretera site, from the Villar del Arzobispo Fm. at Galve, Teruel (Royo-Torres and Canudo, 2003; Canudo et al., 2005). Those teeth were referred to Diplodocidae with doubt by Royo-Torres and Canudo (2003) and to Diplodocoidea by Canudo et al. (2005), but Mannion et al. (2012) proposed a more cautious position related them to the Neosauropoda clade.

Martínez et al. (2000) referred the presence of a camarasaurid tooth (MUJA-0635) from the Lastres Formation at Villaviciosa, Asturias. Posteriorly, Royo-Torres et al. (2009) attributed this tooth to the clade Turiasauria. The absence of a complex cingulum and lingual facets, and the presence of a convex mesial and distal edges on the base of the crown in labial/lingual view do not support the assignation of this tooth to the spatulate-shaped morphology common in *Camarasaurus* (e.g. Gilmore, 1925), and support Royo-Torres et al. (2009) taxonomic approach.

Although the presence of pencil- and heart-shaped teeth on the Upper Jurassic-basal Lower Cretaceous of Spain, one compressed cone-chisel teeth were reported close the *Aragosaurus* fossil-site. *Aragosaurus ischiaticus* is a basal camarasauromorph (Mannion et al., 2013; Royo-Torres et al., 2014a) although the presence of some affinities with Titanosauriformes (e.g. Canudo et al., 2001; D'Emic, 2012). This tooth described in detail by Canudo et al. (2001) is particularly similar with some of the teeth assigned to the morphotype I (e.g. Fig. 6.9c) proposed here for the Portuguese Upper Jurassic compressed cone-chisel-shaped teeth.

Figure 6.16. Temporal patterns in sauropodomorph tooth shape following Chure et al. (2010) incorporating the heart-, spatulate, compressed cone-chisel-shaped and pencil-shaped teeth from the Upper Jurassic of the Lusitanian Basin. The plot shows the tooth slenderness index for sauropodomorph genera throughout the Mesozoic. Orange field indicates non-sauropod sauropodomorphs, brown field indicates basal sauropods, pink field indicates diplodocoids, and blue field indicates macronarians. The problematic phylogeny of Jobaria is indicated by cross-hatching; the transparent blue and brown fields indicate the shape of the tooth space when *Jobaria* is included within macronarians and basal sauropods, respectively. Time scale based on Gradstein et al. (2004). Symbology for Portuguese teeth morphotypes: the yellow, green and red circles represent the average Log10SI for morphotype I, II, and III of the heart-shaped morphotype, respectively; the black star represent the average Log10SI of the spatulate morphotype; the yellow, green and red square represent the average Log10SI for morphotype I, II, and III of the compressed cone-chisel-shaped morphotype; and white circle represent the average Log10SI of the pencil-shaped morphotype.

At the moment, on the Spanish Upper Jurassic record is possible to identify three main morphotypes, heart-, pencil- and compressed cone-chisel-shaped teeth. As in the Portuguese Upper Jurassic, the paleobiodiversity recorded for sauropods on this territory is in accordance with the present tooth morphology variability, including turiasaurs (*Turiasaurus riodevensis* and *Losillasaurus giganteus*), basal macronarians (*Aragosaurus*) and diplodocids (e.g. Sanz et al., 1987; Casanovas et al., 2001; Sanchéz-Hernández, 2005; Ortega et al., 2006; Royo-Torres et al., 2006, 2007, 2009, 2014a; Barco, 2009; Canudo et al., 2010; Cobos et al., 2011; Royo-Torres and Upchurch, 2012; Suñer et al., 2014). The presence of spatulate-shaped teeth is not confirmed, and will be, for the moment, considered absent in the Spanish Upper Jurassic record. The phylogenetic placement of *Galveosaurus* is uncertain. It has been considered as a cetiosaurid (Sánchez-Hernández, 2005), a basal eusauropod (Canudo et al., 2006), as a possible neosauropod (Barco et al., 2005), suggesting its inclusion in Diplodocoidea (Barco, 2005) or in Macronaria (Barco et al., 2006). Finally, *Galveosaurus* has been considered as a non-titanosauriform macronarian (Barco, 2009; Barco et al., 2009; Carballido et al., 2011; Carballido and Sander, 2014; Mannion et al., 2013) or a putative basal titanosauriform with brachiosaurid affinities (D'Emic, 2012). If *Galveosaurus* is confirmed as a titanosauriform, this can be in accordance with the presence of compressed cone-chisel-shaped teeth on the Spanish Upper Jurassic record.

The Upper Jurassic sediments of the Morrison Formation provided an impressive number of sauropods specimens, corresponding to the best-known Upper Jurassic sauropod faunas (e.g., Marsh, 1878; Osborn, 1899, 1904; Hatcher, 1901, 1903; Riggs, 1903; Lull, 1919; Osborn and Mook, 1921; Gilmore, 1925, 1936; Ostrom and McIntosh, 1966; Jensen, 1987; McIntosh and William, 1988; McIntosh et al., 1996a, b; Wilson, 1999; Ikejiri, 2004, 2005; Harris and Dodson, 2004; Ikejiri et al., 2005; Lucas et al., 2006; Lovelace et al., 2007; Tschopp and Mateus, 2013; Tschopp et al., 2015). The spatulate- and pencil-shaped teeth are particularly abundant in the Morrison Fm. record and they have been found in association with cranial and postcranial material of the camarasaurid *Camarasaurus* and the flagellicaudatans *Diplodocus*, *Suuwassea* and *Apatosaurus* (e.g. Holland,1924; Gilmore, 1925; Berman and McIntosh, 1978; Madsen et al., 1995; Whitlock, 2010). Carpenter and Tidwell (1998) described a brachiosaurid skull, but the associated teeth are described as more likely to spatulate-shaped morphotype, which feature the *Camarasaurus* genus. The Morrison Fm. presents similar sauropod faunas when compared with the Iberian Upper Jurassic record being composed by flagellicaudatans, camarasaurids, brachiosaurids (e.g. Wilson and Sereno, 1998; Wilson, 2002; Upchurch et al., 2004; Harris, 2006) and *Haplocanthosaurus* with an uncertain phylogeny (e.g. Wilson and Sereno, 1998; Wilson, 2002; Upchurch et al., 2014; Harris, 2006; Carballido et al., 2011; Carballido and Sander, 2014). The presence of shared genus between Morrison Fm. and the Upper Jurassic of Portugal has been suggested several times for sauropods (Wilson and Sereno, 1998; McIntosh, 1990a,b; Mateus, 2006; Tschopp et al., 2015) and non-sauropod dinosaurs (Galton, 1980; Pérez-Moreno et al., 1999; Mateus and Antunes, 2000a, b; Mateus, 2006; Mateus et al., 2006; Ortega et al., 2006, 2009; Escaso et al., 2007; Malafaia et al., 2007, 2010, 2015; Hendrickx and Mateus, 2014). Proposed phylogenetic approaches support the similitudes between Portuguese and North American taxa (Mannion et al., 2012; Tschopp and Mateus, 2013; Mocho et al., 2014a; Tschopp et al., 2015). Nevertheless, the present state of knowledge still supports the exclusivity of Portuguese Upper Jurassic taxa, *Lourinhasaurus alenquerensis*, *Lusotitan atalaiensis*, *Zby atlanticus* and *Dinheirosaurus lourinhanensis* (Mannion et al., 2012, 2013; Mocho et al., 2014a; Mateus et al., 2014a). Tschopp et al. (2015) proposed the inclusion of *Dinheirosaurus* within the Morrison Fm. genus, *Supersaurus*. The presence of heart-shaped teeth have not been reported yet for the Morrison Fm., as well as, material with turiasaur affinities. For the moment, during the Upper Jurassic, turiasaurs seems to be restricted to the European territory, as well as, the heart-shaped teeth morphology (Royo-Torres et al., 2014b, Mocho et al., in press).

From Tendaguru Formation, the most common teeth morphotypes are assigned to pencil- and compressed cone-chisel-shaped teeth, and related with the brachiosaurid *Giraffatitan* and the dicraeosaurid *Dicraeosaurus* (Janensch, 1936). So far, they have not been described spatulate- and heart-shaped teeth for the Tendaguru Fm. (Janesnch, 1936, pers. observ., PM).

6.8. CONCLUSIONS

The present work describes and discusses a sample of sauropod teeth collected from the sediments from Upper Jurassic of the Lusitanian Basin (Portugal). On the studied sample, four main tooth morphologies were identified: heart-, spatulate-, compressed cone-chisel- and pencil-shaped teeth. For the heart- and compressed cone-chisel-shaped teeth were defined three different morphotypes for each main morphology.

The heart-shaped teeth have been described in detail in previous studies, being defined three distinct morphotypes. Some small differences are found on the wrinkling pattern along the three morphotypes, and the observed crown morphological variability could be positional or ontogenetic related (Mocho et al., 2012, in press). The spatulate-shaped teeth also present some morphological variability possibly related with a different position on the tooth row. The presence of a complex cingulum (presence of more than one lingual facet, a medial ridge and rounded bosses) suggests the placement of these teeth in Macronaria. No great differences were found on the wrinkling pattern. The proposed sequence of wear for this type morphology is the early appearance of the distal wear facet, after, the mesial one, and later, the apical facet.

For the compressed cone-chisel-shaped teeth were defined three distinct morphotypes. The morphological variability on the overall morphology of the crown and on the wrinkling pattern might be explained by different positions on the tooth row or by different ontogenetic stages. This morphology is exclusive of basal titanosauriforms and the presence of a apex that twisted axially through an arc more than 45° in some teeth, suggests that some of them might pertain to Brachiosauridae. Heart-, spatulate- and compressed cone-chisel-shaped teeth are placed within the teeth morphospace occupied by non-neosauropod and macronarian sauropods during the Upper Jurassic.

The pencil-shaped teeth are scarce and new founds are necessary to improve the significance of the hypothesis provided by this study. The SI values of these specimens are higher, but do not fits in the morphospace occupied by other diplodocids. This could be explained by the presence of some wear. The general morphology (sub-cylindrical crowns, oval wear facet on the labial side, higher SI values and the absence of carinae), and assuming the global absence of derived titanosauriforms on the Upper Jurassic (e.g. D'Emic, 2012; Mannion et al., 2013; Carballido and Sander, 2014), it is possible to relate tentatively these teeth to Diplodocoidea.

In conclusion, the present sample including undescribed and classical specimens suggest for the presence of non-neosauropod eusauropods, probably related with Turiasauria (heart-shaped teeth); basal macronarians (spatulate-shaped teeth); basal titanosauriforms (compressed cone-chisel-shaped teeth); and diplodocoids (pencil-shaped teeth). This is in accordance with the known diversity for the Portuguese Upper Jurassic sauropod faunas, which includes the turiasaur *Zby*, the diplodocid *Dinheirosaurus* and basal macronarians *Lourinhasaurus* (a camarasaurid) and *Lusotitan* (a brachiosaurid with doubt).

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CHAPTER 7

New data about Upper Jurassic sauropods of the central and northern part of the Bombarral Sub-basin (Lusitanian Basin, Portugal)

New data on Upper Jurassic sauropods of central and northern sectors of the Bombarral Sub-basin (Lusitanian Basin, Portugal)

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7.1. INTRODUCTION

The Upper Jurassic sediments of the Lusitanian Basin (Portugal) are known by the abundant occurrences in fossil vertebrates, particularly dinosaurs, turtles and crocodyliforms (e.g. Sauvage, 1897-98; Lapparent and Zbyszewski, 1957; Dantas, 1990; Antunes and Mateus, 2003; Mateus, 2006; Ortega et al., 2006, 2009, 2013). Sauropods are so far represented by four taxa: the camarasaurid *Lourinhasaurus alenquerensis* (Lapparent and Zbyszewski, 1957; Dantas et al., 1998; Mocho et al., 2013a, 2014a); the diplodocid *Dinheirosaurus lourinhanensis* Bonaparte and Mateus (1999) (Mannion et al., 2012), the brachiosaurid *Lusotitan atalaiensis* (Lappatent and Zbyszewski, 1957; Antunes and Mateus, 2003; Mannion et al., 2013), and the turiasaur, *Zby atlanticus* Mateus, Mannion and Upchurch, 2014.

Several classical (Sauvage, 1897-98; Lapparent and Zbyszewski, 1957) and recent occurrences (e.g. Dantas et al., 1992; Bonaparte and Mateus, 1999; Rauhut, 2000; Royo-Torres et al., 2006, 2009; Yagüe et al., 2006; Mateus, 2009; Ortega et al., 2010; Mannion et al., 2012; Mocho et al., 2012, 2013b, 2014a, b; Mateus et al., 2014) have been referred, denoting higher sauropod diversity in the Lusitanian Basin during the Upper Jurassic. The presence of turiasaurs in Portuguese Upper Jurassic record was firstly suggested by Royo-Torres et al. (2006), and posteriorly corroborated by the presence of teeth and postcranial material (Mateus, 2009; Royo-Torres et al., 2009; Ortega et al., 2010; Mocho et al., 2012, in press; Mateus et al., 2014). A new turiasaurian taxon, *Zby atalanticus*, was established from a specimen found in Vale de Pombas (Lourinhã) (Mateus et al., 2014).

The vertebrate faunas of the Portuguese Upper Jurassic record are mainly recorded in the Upper Jurassic to Lower Cretaceous sequence deposited in the Lusitanian Basin during the 3rd rifting episode (e.g. Rasmussen et al., 1998; Kullberg et al., 2006).This period was marked by the internal differentiation of the Central Sector of the Lusitanian Basin into several sub-basins (Turcifal, Arruda and Bombarral Sub-basins) and followed by an important siliciclastic input that progressively infilled these basins (Pena dos Reis et al., 2000). Above the Kimmeridgian, the sedimentary sequence is strongly siliciclastic with a continental signature at the top of the sequence (Hill, 1988). Taylor et al. (2013) proposed the subdivision of the Bombarral Sub-basin into two sub-basins, Bombarral-Alcobaça and Consolação Sub-basins.

The northern sector of the Bombarral Sub-basin (see Kullberg, et al., 2006) is relatively scarce in dinosaur fossil remains, highlighting three important localities (Fig. 7.1): Andrés in Pombal (Pérez-Moreno et al., 1999; Malafaia et al., 2010), the Guimarota coal mine in Leiria (e.g. Hahn, 1971; Bräm, 1973; Seiffert, 1973; Thulborn, 1973; Krusat, 1980; Broschinski, 2000; Rauhut, 2000) and Casal Novo in Batalha (Escaso et al., 2007). In Andrés, it was found a partial disarticulated theropod skeleton, including cranial elements, referred to *Allosaurus fragilis* (Peréz-Moreno et al., 1999). Several other groups are also represented such as fishes, sphenodonts, crocodyliforms, pterosaurs, and at least, seven forms of dinosaurs (Malafaia et al., 2010). Sauropods are represented by isolated teeth and some postcranial remains related to Turiasauria, Diplodocidea and Titanosauriformes (Malafaia et al., 2010). The Guimarota mine is one of most relevant Upper Jurassic quarries of the Iberian Peninsula, being recover a diverse fossil assemblage, including dinosaurs (ornithopods, theropods and sauropods), mammals, pterosaurs, fishes, crocodyliforms, amphibians and lepidosaurs (Hahn, 1971; Bräm, 1973; Seiffert, 1973; Thulborn, 1973; Krusat, 1980; Broschinski, 2000; Gassner, 2000; Hahn and Hahn, 2000; Krebs, 2000; Krebs and Schwarz, 2000; Kriwet, 2000; Martin, 2000; Martin and Nowotny, 2000; Rauhut, 2000; Wiechmann, 2000; Wiechmann and Gloy, 2000; Caldwell et al., 2015). The sauropods are relatively poorly represented in the Guimarota mine, with five compressed cone-chisel-shaped teeth related to Brachiosauridae (Rauhut, 2000, 2001) or to cf.

Lusotitan atalaiensis (Mateus, 2005). In Casal Novo (Batalha municipality) was found several remains of a stegosaurian individual related to *Stegosaurus* (Escaso et al., 2007).

Some unpublished sauropod occurrences from the central region of Portugal are reported and described herein (S.5). The described material was found at the north of the Maciço Calcário Estremenho (MCE) close to Pombal, Batalha, Porto de Mós and Leiria (Fig. 7.1), and in a sector located to the east of MCE and next to Caldas da Rainha and São Martinho do Porto (Fig. 7.1; the coastal cliffs of São Martinho to Foz do Arelho are considered part of the Consolação Sub-basin *sensu* Taylor et al., 2013). These specimens are deposited in the paleontological collections of the Muséum national d'Histoire naturelle (Paris, France), Museu Geológico (Lisboa) and Museu Municipal de Porto de Mós.

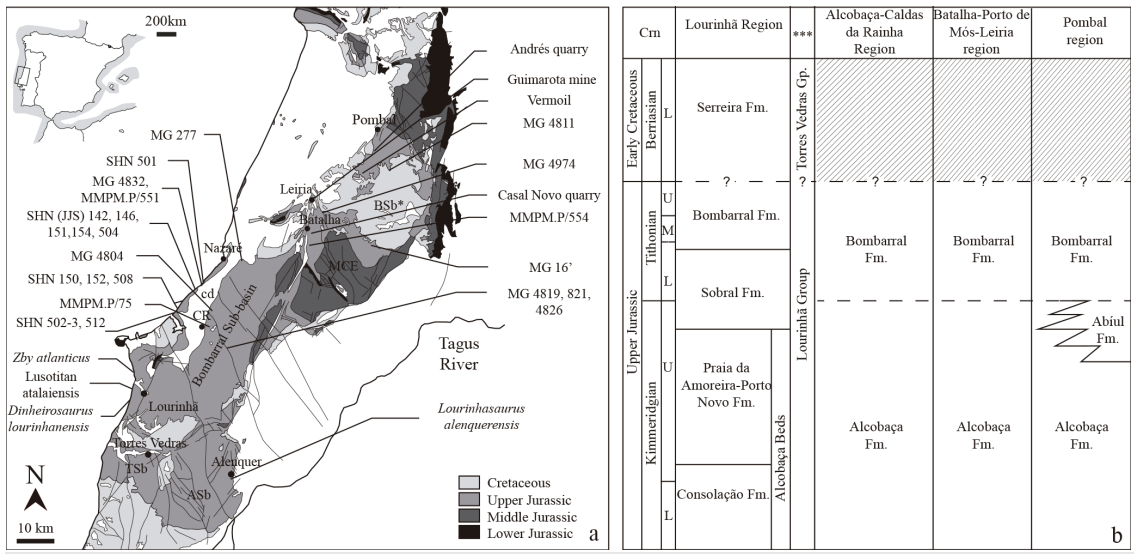

Figure 7.1. a. Geological map (adapted from Oliveira et al., 1992) showing the Portuguese Mesozoic levels and the localities of the material collected in the central and northern region of the Bombarral Sub-basin. b. Stratigraphiy of Bombarral Sub-basin in Lourinhã region (based on Manuppella et al., 1999), Caldas da Rainha-Alcobaça region (Kullberg et al., 2006; Azerêdo et al., 2010) Batalha-Porto de Mós-Leiria region (based on Manuppella et al., 2000; Kullberg et al., 2006; Escaso et al., 2007) and Pombal region (Kullberg et al., 2006; Malafaia et al., 2010).Crn – Chronostratigraphy; **sensu* Kullberg et al., 2006; ****sensu* Yagüe et al., 2006;'the locality is not precise; ASb- Arruda Sub-basin; BSb – Bombarral Sub-basin, cd – Caldas Diapir; CR – Caldas da Rainha town; MCE – Maciço Calcário Estremenho; TSb – Turcifal Sub-basin.

7.2. ANATOMICAL ABBREVIATIONS

aca, anterior chevron articulation; ant. spdl, anterior spinodiapophyseal lamina; asp, ascending process; aspa, articular surface for the ascending process; cdf, centrodiapophyseal fossa; cr, caudal rib; f, fossa; fia, fibular articular surface; lat. spol, lateral spinopostzygapophyseal lamina; med. spol, medial spinopostzygapophyseal lamina; na, neural arch; paf, posterior astragalar fossa; pafc, crest in posterior astragalar fossa; pca, posterior chevron articulation; pcdl, posterior centrodiapophyseal lamina; pl, pleurocoel; pcpl, posterior centroparapophyseal lamina; pocdf, postzygapophyseal centrodiapophyseal fossa; post. spdl, posterior spinodiapophyseal lamina; posl, postspinal lamina; poz, postzygapophyses; prsl, prespinal lamina; sdf, spinodiapophyseal fossa; spof, spinopostzygapophyseal fossa; spol-f, spinopostzygapophyseal lamina fossa; sprf, spinoprezygapophseal fossa; sprl, spinoprezygapophyseal lamina; tb, tuberosity; tap, triangular alliform process; tia, tibial articular surface; tprl, intraprezygapophyseal lamina; vh, ventral hollow.

7.3. INSTITUTIONAL ABBREVIATIONS

MG, Museu Geológico, Laboratório Nacional de Energia e Geologia, Lisboa, Portugal; MMPM/P, paleontological collections of the Museu Municipal de Porto de Mós, Porto de Mós, Portugal; MNHN, Muséum national d'histoire Naturelle, Paris, France; SHN, Sociedade História Natural, Torres Vedras, Portugal [plus (JJS) for the José Joaquim dos Santos collection deposited in the Sociedade de História Natural].

7.4. POMBAL

An appreciable outcropping area of Alcobaça and Bombarral Formations extends south of the city of Pombal. Near Pombal, some theropod remains were attributed to *Megalosaurus insignis* Eudes-Deslongchamps (1870) and *Megalosaurus pombali* Lapparent and Zbyszewski (1957) by Lapparent and Zbyszewski (1957), and now considered as indeterminate theropods (Mateus, 2000). The most important fossil-site in this area is the locality of Andrés in Santiago de Litém (Pérez-Moreno et al., 1999), in which has been identified a great and diverse accumulation of vertebrates from the Bombarral Fm. (Malafaia et al., 2010). The dinosaur content is mainly represent by an allosauroid theropod attributed to *Allosaurus fragilis* Marsh (1877) by Peréz-Moreno et al. (1999). Nevertheless, based on the more recent description of the new species, *A. europaeus* Mateus et al. 2006, the previously identification should be taken with caution pending a detailed description of new elements collected in Andrés site (Malafaia et al., 2007, 2010, pers. observ., EM). Several other dinosaur groups are present such as dromaeosaurids, camptosaurids and dryosaurid ornithopods, and sauropods. In the Andrés quarry were collected teeth and postcranial material assigned to Sauropoda. A preliminary analysis allows identifying four tooth morphotypes: heart-, spatulate-, compressed cone-chisel-, and pencil-shaped teeth; that can be attributed to Diplodocoidea, Turiasauria and Titanosauriformes (Malafaia et al., 2010). Other vertebrate groups are recorded in Andres, such as fishes, sphenodonts, crocodyliforms and pterosaurs (Malafaia et al., 2010). In the paleontological collections of the Muséum national d'Histoire naturelle was identified a still unpublished dorsal neural spine found next to Vermoil (Fig. 7.2, MNHN.unnumbered). The sauropod remains in this region are relatively scarce and this specimen will be described and discussed.

7.4.1. Vermoil material

Material: Partial neural arch of a middle or posterior dorsal vertebra (Fig. 7.2) deposited in the Paleontological collections of the Muséum national d'Histoire naturelle (unlabeled specimen).

Locality and horizon: The label associated to the specimen refers: "Vermoil and Vale de Lagares. South of Vermoil". In Vermoil area there is a place called Lagares, where the Lagares River flows. This river intersects the sediments of Bombarral Formation, considered as lower-upper Tithonian in age (Marques et al., 1992; Manuppella et al., 2000; Malafaia et al., 2010).

Description: A relative complete and isolated neural spine, lacking the ventral part of pedicels and prezygapophyses (Fig. 7.2). The neural spine is transversely constricted at the base, and expands transversely in its distal part. The left postzygapophysis is almost complete unlike the right one. Its ventral surface is flat with a sub-squared outline, and slopes 10º-20º ventromedially. On the neural arch is possible to identify several laminae and fossae. The dorsal section of the pcdl is preserved, and borders anteriorly the postzygapophyseal centrodiapophyseal fossa (pocdf, Fig. 7.2e, g, h). In the pocdf there is a short, stout and subvertical lamina, interpreted has a centropostzygapophyseal lamina (cpol). On the medial and lateral side there are two small subfossae, being the medial subfossae deeper than the lateral one. This medial subfossa extends medially and dorsally into the neural arch, occupying a position in the front to the hyposphene

complex. The dorsalmost part of this fossa is below the ventralmost part of the sdf3 (see bellow). These fossae are separated by the podl, particularly thin in this region. The hyposphene complex is not preserved, but its base is transversely thick, suggesting the presence of a well-developed hyposphene, probably with rhomboid shape. Just below to this structure there is a subfossa bordered by two subvertical laminae (also incomplete) that probably correspond to the internal cavities of the neural arch. The anterior sector of the neural arch up to the pcdl is not well preserved. There are two accessory laminae in the centrodiapophyseal fossa (cdf). This fossa is limited by the pcdl posteriorly, and the prdl dorsally. The acpl and ppdl laminae are not preserved.

The lateral face of the neural spine is flat and limited anteriorly by the spinoprezygapophyseal lamina (sprl) and by a stout and single spinopostzygapophyseal lamina (spol). The two laminae delimit laterally a spinodiapophyseal fossa (sdf), ventrally bordered by the prezygodiapophyseal (prdl) and the postzygodiapophyseal (podl) laminae. The ventral sector of this fossa is subdivided in three fossae (sdf1, sdf2 and sdf3, Fig. 7.3) by the presence of two spinodiapophyseal laminae: the anterior spinodiapophyseal lamina (ant. spdl) and the posterior spinodiapophyseal lamina (post. spdl). Sdf1 is smooth and has a subtriangular outline, being limited by the sprl, ant. spdl and prdl, anteriorly, posteriorly and ventrally respectively. The sdf2 is dorsoventrally elongated and corresponds to the widest fossa. This fossa occupies the dorsal part of the neural spine lateral surface. Sdf2 is bordered by the ant. spdl, post. spdl and prdl, anteriorly, posteriorly and ventrally respectively. On the dorsal part of this fossa, there is a smooth subfossa (on both sides) near the apex. Sdf3 bears a triangular outline and is not so extensive dorsoventrally than sdf2, due to the connection between the spol and the post. spdl. Sdf2 and sdf3 are particular deep. The ventral sector of the sdf1 is not preserved. The contact between the spol and the post. spdl is placed ventrally and well separated from the triangular process. The dorsal surface of the neural spine is rough and has a straight outline in posterior view. The dorsal surface of the neural spine runs from the lateral surface to the rough lateral margins of the triangular process (laterally sloping, ≈80º). In dorsal view, the anterior part of the neural spine summit is transversely constricted, above the prespinal process, resulting in a T-shaped profile. The triangular process is located in the posterior region of the neural spine summit. In posterior view, the complex spol+post. spdl corresponds to the lateralmost border of the neural spine as occur in several other sauropods, such as *Camarasaurus*, *Spinophorosaurus* or *Eucamerotus*. This complex diverges laterally up to the triangular process (e.g. Osborn and Mook, 1921; Ostrom and McIntosh, 1966; Blows, 1995; Remes et al., 2009). These laminae are also visible in anterior view. The spinopostzygapophyseal fossa is border by the spol+post. spdl and spol, dorsally and ventrally, respectively. In this fossa, there is a wide, superficial and rough postspinal process (or postspinal lamina), not as developed as the postspinal lamina of diplodocids (e.g. Hatcher, 1901; Wilson, 1999). This process is present along the entire height of the spine except the ventralmost part, between the postzygapophyses. In the anterior face of the neural spine there is a well-developed prespinal lamina (prsl) with a rough surface. In anterior view, the ventral region of the neural spine is not well preserved. Herein, midline scars represented the prsl. Two main laminae split from this prsl: the ant. spdl and an anterior lamina interpreted as a spinoprezygapophyseal laminae (sprl). At the base of the neural spine, between the sprl there is a smooth spinoprezygapophyseal fossa (sprf).

Discussion: Comparing the described neural spine with several complete or partial series of dorsal vertebrae (e.g. Hatcher, 1901, 1903; Osborn and Mook, 1921; Gilmore, 1925, 1936; Janensch, 1929, 1950; McIntosh et al., 1996a; 1996b; Mannion et al., 2012) it can be considered that pertain to a middle or posterior dorsal vertebra. The laminae and fossae developed on the neural arches of the dorsal vertebrae are particular diagnostic for sauropods (e.g. Wilson, 1999, 2012a; Wilson et al., 2011), although its interpretation is complex in some cases (e.g. Wilson, 2012b).

A neural spine broader transversely than anteroposteriorly was considered a synapomorphy of the Eusauropoda (Wilson, 2002). Some authors propose that this character is a synapomorphy for Eusauropoda just if is formulated for the most posterior dorsal vertebrae (Carballido and Sander, 2014). In some basal non-eusauropod sauropods, as *Barapasaurus* (Bandyopadhyay et al., 2010) or *Tazoudasaurus* (Allain and Aquesbi, 2008), the anteroposterior length is almost equal to the transverse width. In the Vermoil specimen, the transverse width of the neural spines is clearly higher than the anteroposterior length. However, it is not possible to ensure that this neural spine belongs to one of the last dorsal vertebrae. Transversely broader dorsal neural spines are also shared with several other eusauropods such as *Cetiosaurus* (Upchurch and Martin, 2003; pers. observ., PM), *Spinophorosaurus* (pers. observ., PM), *Haplocanthosaurus* (Hatcher 1903), and neosauropods (e.g. Wilson, 2002; Carballido and Sander, 2014), with the exception of material belonging to *Lapparentosaurus* (subadult and adult remains are unknown, Bonaparte et al., 1986) and *Jobaria* (Sereno et al., 1999).

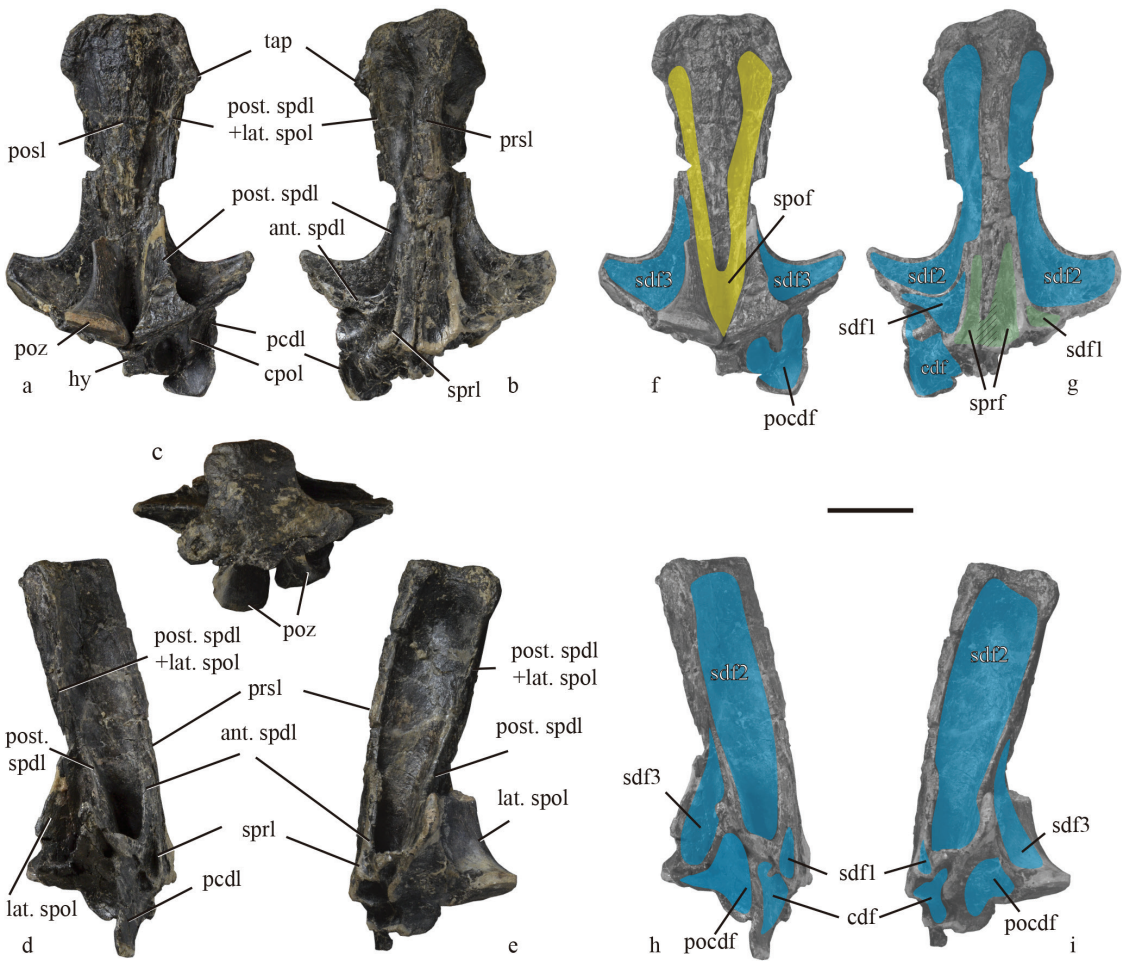

Figure 7.2. Posterior or middle dorsal neural spine (MNHN.unnumbered) from Vermoil (Pombal) in (a) and (f) posterior, (b) and (g) anterior, (c) dorsal, (d) and (h) right, (e) and (i) left views. The fossae present in this neural spine are indicated in blue (diapophyseal fossae), yellow (postzygapophyseal fossae) and green (prezygapophyseal fossae) (*sensu* Wilson et al., 2011) in (f-i).Scale bar: 5cm. See Anatomical abbreviations for abbreviations.

Comparing with the Iberian taxa, the Vermoil specimen shares the transverse expansion of the neural spine with *Losillasaurus* (Casanovas et al., 2001), *Turiasaurus* (Royo-Torres et al., 2006) and probably *Lourinhasaurus* (Mocho et al., 2014a). The dorsal neural spines of *Aragosaurus*, *Zby* and *Lusotitan* are not preserved (Lapparent and Zbyszewski, 1957; Sanz et al., 1987; Mannion et al., 2013; Mateus et al., 2014; Royo-Torres et al., 2014). Mannion et al. (2012) described the presence of transversely compressed neural spines in *Dinheirosaurus*, but the condition is not observable in the type material, being necessary more preparation to confirm it.

The Vermoil spine also presents a well-developed prespinal lamina. This feature is absent in most basal sauropods (Allain and Aquesbi, 2008) and in some basal eusauropods, such as *Cetiosaurus* (Upchurch and Martin, 2003; Carballido and Sander, 2014). This prespinal lamina is rough and wide and extends as a well-defined structure up to the ventral half of the neural spine. This type of prespinal lamina morphology is also found in other eusauropods such as *Turiasaurus* (Royo-Torres et al., 2006); *Losillasaurus* (Casanovas et al., 2001; Barco, 2009); *Giraffatitan* (Janensch, 1950); *Haplocanthosarurs* (Hatcher, 1903; Carballido and Sander, 2014); or *Tastavinsaurus* (Canudo et al., 2008; Royo-Torres, 2009). This condition differs from *Europasaurus* (Carballido and Sander, 2014) and *Galveosaurus* (Barco, 2009) in which the prespinal lamina reaches the base of the neural spine.

The spol of the Vermoil specimen is not bifurcated at the base of the postzygapophysis. A bifurcated spol on middle and posterior dorsal vertebrae was considered as a synapomorphy of *Barapasaurus* + (*Patagosaurus* + ((Omeisauridae) + (*Jobaria* + Neosauropoda))) and for Nemegtosauridae + (‘*T.*’ *colberti* +Saltasauridae) by Wilson (2002). Some authors proposed that the shared condition is restricted to the posterior dorsal vertebrae (Whitlock, 2011). Whitlock (2011) considered that bifurcated spol in posterior dorsal vertebrae is a synapomorphy of Rebbachisauridae. In their data matrix, Carballido et al. (2012) defined a new character based on the presence of a med. spol. (character #172). The presence of a med. spol is restricted to non-dicraeosaurids diplocoids and the brachiosaurids *Giraffatitan*, *Brachiosaurus* and the titanosaur *Rapetosaurus* (see Riggs, 1903; Janensch, 1950; Curry Rogers, 2009; Carballido and Sander, 2014). The Vermoil neural spine presents a simple spol (=lat. spol) and no evidences of a med. spol. The med. spol is also absent in *Turiasaurus* and *Losillasaurus*, but is present in *Galveosaurus*. In short, from postzygapophyses, the spol could be simple, with a single spol lamina such as in Vermoil specimen, *Spinophorosaurus*, *Turiasaurus* or *Losillasaurus*; or with a slight bifurcation, resulting in a second laminae structure (med. spol) as in *Giraffatitan* or *Galveosaurus*, bordering a slight concavity in the dorsal surface of the postzygapophyses process (spinoposzygaposeal lamina fossa, spol-f). Nevertheless, only in some rebbachisaurids is possible to find well-developed med. spol and lat. spol and a well-defined and deep spol-f between them as in *Histriasaurus*, *Rebbachisaurus* and *Nigersaurus* (see codification of Mannion et al., 2012; Wilson, 2012a).

As in many other sauropods, the Vermoil neural spine is simple, without any evidence of bifurcation as occur in the middle and posterior neural spines of *Camarasaurus* (Osborn and Mook, 1921) or *Lourinhasaurus* (Mocho et al., 2014a). Turiasaurs present a particular morphology: a triangular concavity near the anterodorsal and posterodorsal margin of the dorsal neural spine, which could be related with the presence of bifurcated neural spines on the cervical and anterior dorsal vertebrae, as occur in *Turiasaurus riodevensis* Royo-Torres et al. (2006). This feature is absent in the Vermoil sauropod. The absence of bifurcation allows to differentiate it from the diplodocids with bifurcated dorsal neural spines, such as *Diplodocus* (Hatcher, 1901), *Apatosaurus* (Gilmore, 1936) or *Barosaurus* (Lull, 1919; McIntosh, 2005), and from the dicraeosaurids such as *Dicraeosaurus* (Janensch, 1929), *Brachytrachelopan* (Rauhut et al., 2005) and *Amargasaurus* (Salgado and Bonaparte, 1991). The presence of bifurcation in more anterior dorsal vertebrae is not excluded in the taxon to which the neural spine of Vermoil belongs. In *Lusotitan*, *Aragosaurus* and *Zby*, the presence of bifurcated neural spines is unknown due the absence of preserved dorsal

neural spines. In *Dinheirosaurus*, more preparation of the holotype is required to confirm or refute the absence of bifurcation, proposed by Mannion et al. (2012).

Vermoil specimen present two spdl laminae, the ant. spdl and the post. spdl, they are a common feature within sauropods (Wilson, 2012a). The ant. spdl is less developed than the post. spdl, and has some similarities with the sprl of *Giraffatitan* or *Turiasaurus*. In these two sauropods, the sprl follows a similar orientation of the ant. spdl in the Vermoil sauropod (in the left side ant. spdl overlaps with the sprl) but its ventral end deflects laterally to the transverse process. The junction of the post. spdl and the spol is ventral to the triangular aliform process as occur in *Galveosaurus*, *Giraffatitan*, *Brachiosaurus*, *Haplocanthosaurus*, *Turiasaurus* (Carballido and Sander, 2014) and *Eucamerotus* (pers. observ., PM). The presence of a transversely expanded neural spine in middle or posterior dorsal vertebrae and the presence of well-defined prespinal laminae (at least in the dorsalmost part of the spine) suggest that this sauropod might be placed within Eusauropoda, being considered as an indeterminate eusauropod different to turiasaurs, diplodocids and basal titanosauriforms. Although the combination of recognized characters is not incompatible with their assignment to Macronaria, the incompleteness of the specimen advises a more open determination.

7.5. LEIRIA-BATALHA-PORTO DE MÓS

The Alcobaça and Bombarral Formations also outcrop north of the Maciço Calcário Estremenho (Manuppella et al., 2000). Some fossil-sites have been recognized in Batalha, Vila Nova de Ourém, Leiria and Porto-de-Mós. One of the most relevant accumulations was found in the Guimarota coal mine (e.g. Rauhut, 2000). From the sediments of this mine pertaining to the Alcobaça Fm. (Kimmeridgian-lower Tithonian, Manuppella et al., 2000) were identified several vertebrate groups such as fishes, amphibians, mammals, lepidosauriforms, turtles, crocodyliforms, pterosaurs, and dinosaurs (e.g. Broschinski, 2000; Gassner, 2000; Hahn and Hahn, 2000; Krebs, 2000; Krebs and Schwarz, 2000; Kriwet, 2000; Martin, 2000; Martin and Nowotny, 2000; Rauhut, 2000; Wiechmann, 2000; Wiechmann and Gloy, 2000; Caldwell et al., 2015). Dinosaurs are represented by iguanodontian ornithopods (camptosaurs and dryosaurs), theropods (ceratosaurids, allosaurids, tyrannosauroids, dromaeosaurids and troodontids) including the holotype of *Aviatyrannis jurassica* Rauhut (2003) and a tooth considered as cf. *Archaeopteryx* sp., and sauropods (e.g. Rauhut, 2000; Wiechmann and Gloy, 2000). The Guimarota mine is relatively poor in sauropod remains, being found some small teeth considered Brachiosauridae (Rauhut, 2000, 2001) or cf. *Lusotitan atalaiensis* (Mateus, 2005).

A relevant fossil-site in this area is located at Casal Novo (Batalha) in the sediments of the Alcobaça Formation (Manuppella et al., 2000) with fluvial origin (Escaso et al., 2007). In this site was found a partial stegosaurian individual assigned to *Stegosaurus* (Escaso et al., 2007). Sauropod remains have not been found in Casal Novo.

Lapparent and Zbyszewski (1957) also reported some localities with dinosaur occurrences near Vila Nova de Ourém and Porto de Mós. Two teeth probably related to Turiasauria (Mocho et al., 2012, in press) and to Titanosauriformes were found near Ourém. We will describe here some new occurrences from this area: a partial tail from Abadia (Leiria), a set of sauropod elements probably collected around Batalha, and a posterior caudal vertebra from Fonte do Oleiro.

7.5.1. Abadia material

Material: A partial dorsal centrum and a partial caudal series composed by anterior to middle caudal vertebrae (MG 4974, Figs. 7.3 and 7.4).

Locality and horizon: The label associated to this set referred "Abadia (Batalha)". Abadia is

located to the north of Batalha, and belongs to the Leiria municipality. On this area, the Montejunto Formation contacts a sequence composed by Alcobaça and Bombarral Formations by fault (Teixeira et al., 1966; Manuppella et al., 2000). On Abadia locality outcrops the Bombarral Fm. (fluvial sediments), upper Kimmeridgian-Tithonian in age (Manuppella et al., 2000; Kullberg et al., 2006). Nevertheless is not excluded the possibility of these vertebrae pertain to the Alcobaça Fm. sediments, Kimmeridgian-basal Tithonian in age (Manuppella et al., 2000).

Figure 7.3. Partial dorsal centrum (MG 4974) in (a) posterior and (b) left views. Scale bar: 5cm. See Anatomical abbreviations for abbreviations.

Description: A partial dorsal centrum is preserved, including part of the posterior articulation and the left lateral face (Fig. 7.3). The posterior face is concave, and the lateral face bears a pleurocoel. Only the posterior border of the pleurocoel is preserved. A partial caudal series is preserved including anterior and middle caudal vertebrae (Fig. 7.4). For a relative position of caudal vertebrae, we follows Díez-Díaz et al. (2013) and Tschopp et al. (2015). Four anterior vertebrae with transverse and dorsoventrally short caudal ribs are considered as the last anterior caudal vertebrae. The centra only preserve the base of the neural arches.

The preserved anterior centra are subcircular in anterior and posterior views. The anterior articulation bears a transverse sinform pit in the anterior articulation, not so well defined in the posterior articulation. All centra are amphicoelous, but the posterior face is generally flatter than the anterior one. The posterior face of the anterior centrum is almost flat. The ventral face is short transversely and transits continuously to the lateral face of the centrum. The ventral face is convex and becomes transversely concave in the region between the articulations for the chevrons. Articulations for the chevrons are present next to the anterior and the posterior face of the centrum. The posterior chevron articulations are bigger than the anterior ones. They are rough and sometimes they are concave. In the transition to the middle caudal vertebrae, the anterior articulations for the chevrons become rudimentary and disappear. In the last preserved anterior vertebrae, a longitudinal crest on the lateral face of the centrum appears bellow the caudal rib.

The caudal ribs are dorsoventrally compressed, mainly laterally directed with a slight posterior projection (never reach the posterior articulation in dorsal view). In the most anterior caudal vertebrae, the distal end of the caudal rib bears a marked deflection assuming a posterior orientation. The caudal ribs are not deep but extend to the lateral face of the neural arch. They lack

any lamina structure (the condition in most proximal anterior caudal vertebrae is unknown). The most anterior neural arch bears a hyposphenic ridge. The neural arch is anteriorly displaced. The zygapophyses are not totally preserved but in the most anterior preserved centrum is possible to observe the ventral sector of the sprf limited ventrally by the intraprezygapophyseal lamina (tprl) and laterally by the sprl.

Between the anterior caudal vertebra and the first preserved middle caudal vertebra there is a gap. The middle caudal vertebrae are amphicoelous. The anterior surface becomes flat and the posterior one is more concave than the anterior one. In these vertebrae the longitudinal crest referred above, occupies a more ventral position on the lateral surface of the centrum. The neural arch is slightly displaced anteriorly. The most posterior preserved centra are slightly transversely compressed. The anterior articulations for the chevrons are not present. There are longitudinal rugosities in the place where those articulations appear on the anterior caudal centra. The ventral face is transversely convex and the lateral one is slightly concave.

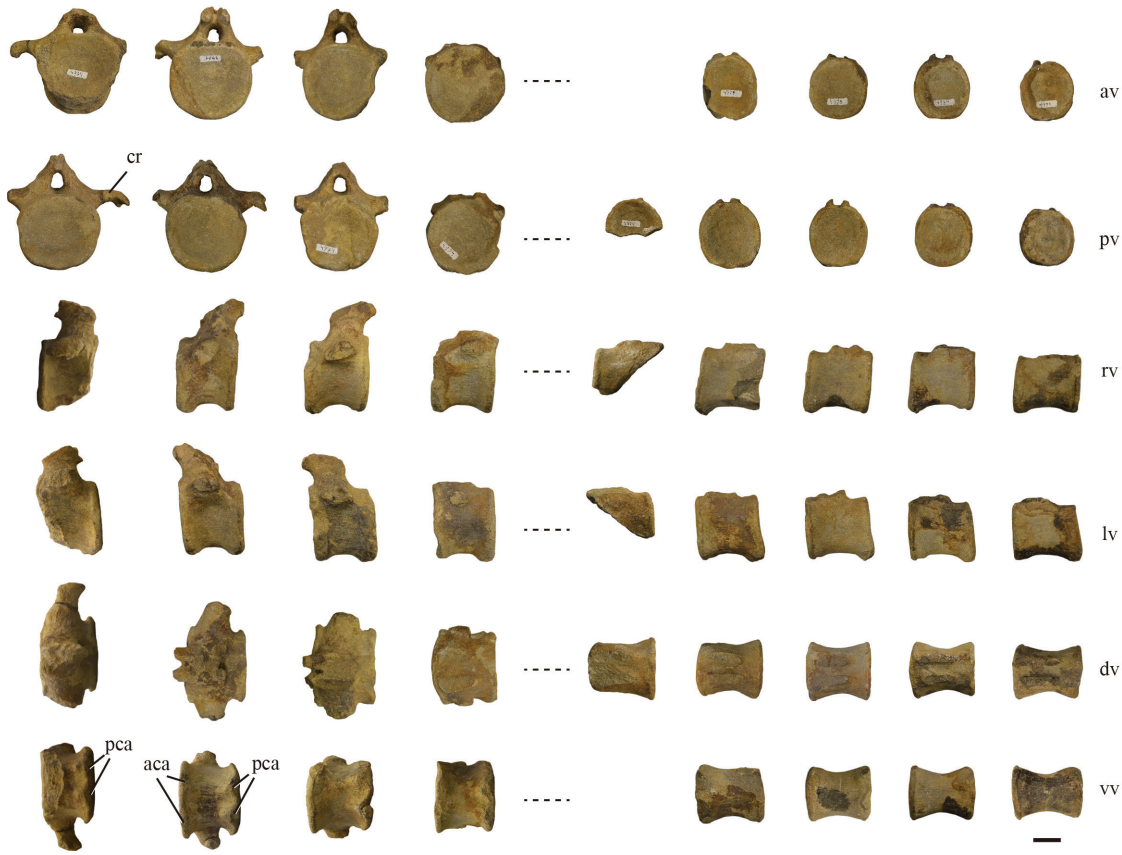

Figure 7.4. Partial caudal series (MG 4974) including anterior and middle caudal vertebrae from Abadia (Leiria) in anterior, posterior, right, left, dorsal and ventral views. Scale bar: 5cm. See Anatomical abbreviations for abbreviations.

Discussion: MG 4974 specimen is incomplete and it has no complete neural arch. The centra are subcircular and do not bear a dorsoventral compression, which is common in basal Titanosauriformes (Janensch, 1950; Tidwell et al., 1999, 2001; Upchurch et al., 2004; Canudo et al., 2008; Royo-Torres, 2009) and in some basal eusauropods (e.g. Upchurch and Martin, 2003). The absence of dorsoventral compressed centra distinguishes MG 4974 from *Lusotitan*

atalaiensis (Mannion et al., 2013) or from the São Bernardino sauropod (MG 4978, Lapparent and Zbyszewski, 1957). The caudal ribs are mainly laterally directed, as is typical in sauropods non-titanosauriforms (D'Emic, 2012; Mannion et al., 2013). The presence of a posterior deflection of the caudal ribs distal end (see dorsal view, Fig. 7.3) is shared with *Tastanvisaurus* (Royo-Torres, 2009). The caudal ribs on the anterior caudal vertebrae are deep as occur in sauropods (Carballido and Sander, 2014). The posterior articulation is successively flatter in more anterior positions, common feature in sauropods that transit to a procoelous condition (e.g. Bonaparte et al., 2000) or in basal macronarians (e.g. Riggs, 1903; Janensch,1950; Tidwell et al., 1999, 2001; McIntosh et al., 1996a, 1996b; Canudo et al., 2008; Royo-Torres, 2009; Mannion et al., 2013; Mocho et al., 2014a; Royo-Torres et al., 2014). Nevertheless, a flat or procoelous condition in Batalha tail could not be confirmed. In conclusion, this partial tail only could be related with indeterminate sauropod with a lot of missing data that do not allow obtaining a more precise taxonomic approach.

7.5.2. Batalha material

Material: The association of this material (MG 30389) is not clear, but they might pertain to the same fossil-site or even to the same individual. The set of elements includes a partial posterior dorsal vertebra, dorsal neural arch fragments (probably from the same vertebra), a partial middle caudal vertebra and an incomplete ischium (Fig. 7.5).

Locality and horizon: This material was found in Batalha, but more details about its precise location are unknown. In this location outcrops two Upper Jurassic formations known by the presence of terrestrial vertebrate fossils (e.g. Escaso et al., 2007), Alcobaça and Bombarral Formations, upper Kimmeridgian-basal Tithonian and upper Kimmeridgian-Tithonian in age, respectively (Manuppella et al., 2000).

Description: A posterior dorsal centrum and part of the neural arch were partially reconstructed (Fig. 7.5a-f). The centrum is amphicoelous, anteroposteriorly short and without evidence of parapophyses suggesting a middle or posterior position in the dorsal series. The ventral face is convex and lacks evidence of sagittal or parasagittal crests. The lateral face are perforated by pleurocoels. The pleurocoels are medially deep and slightly ventrally deep. The bone tissue is polycamerate (following Wedel, 2000, 2003). The base of the neural arch is preserved with the ventral sector of the pcdl and a lamina that is interpreted as the posterior centroparapophyseal lamina (pcpl). In posterior view, the centrum is subcircular bearing a dorsal recess (Fig. 7.5c). Two fragments of the neural spines were recognized both including the postzygapophyes (right and left, Fig. 7.5g-h). The postzygapophyses are flat-to-concave. Two laminae considered as a lateral and medial spinopostzygaphyseal laminae (lat. spol and med. spol) part from the dorsal surface of the postzygapophyses.

A fragment of the posterior region of a middle caudal vertebra is preserved (Fig. 7.5i-n). The posterior face is mainly flat-to-slightly procoelous. The ventral face is transversely concave (ventral hollow *sensu* Wilson, 2002), and seems to be bordered by two ventrolateral ridges, that are broken in this element. The centrum has a quadrangular cross-section. The lateral face bears a wide fossa locally perforated (Fig. 7.5j-k). In posterior view, the centrum probably was subcircular, but the ventral edge of the posterior articulation is not preserved.

A partial right ischium was recovered (Fig. 7.5o-p). The base of the ischiatic peduncle is preserved, and, on the lateral face and near the dorsal edge, there is an anteropoteriorly elongated tuberosity. This tuberosity is ventrally bordered by a groove with the same orientation (Fig. 7.5o). The ischiatic peduncle bears a drop-like outline with a ventral acute edge.

Discussion: The relationships between these elements are not clear and they might represent different individuals and even different fossil sites around Batalha region. The dorsal vertebra

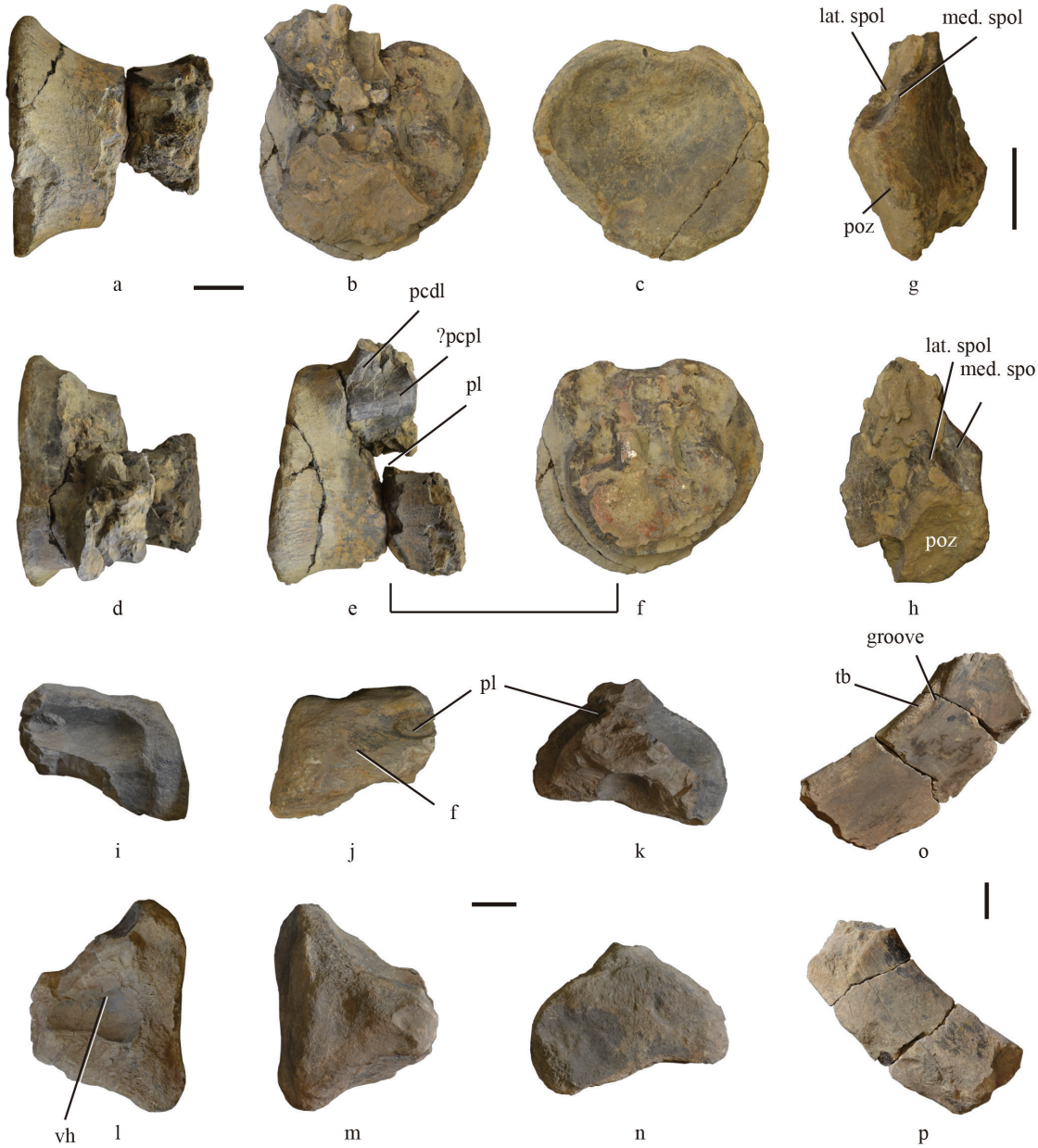

Figure 7.5. Sauropod material from near Batalha. Partial posterior (?) dorsal centrum in (a) ventral, (b) anterior, (c), posterior, (d) dorsal, (e) right views, and a (f) centrum cross-section, showing its internal structure. Fragment of the neural spine in (g) posterior and (h) left views. Middle caudal vertebra in (i) left, (j) right, (k) anterior, (l) ventral, (m) dorsal and (n) posterior views. Partial ischiatic peduncle in (o) lateral and (p) medial views. Scale bar: 5cm. See Anatomical abbreviations for abbreviations.

bears deep pleurocoels as generally occurs in neosauropods such as diplodocoids (excluding Dicraeosauridae, *sensu* Salgado et al., 1997) and basal macronarians (Wedel, 2000, 2003; Upchurch et al., 2004). The presence of deep pleurocoels was considered a diagnostic feature of *Omeisaurus*+Neosauropoda by Wilson and Sereno (1998). This type of pleurocoels is present in *Camarasaurus* (e.g. Osborn and Mook, 1921; Ostrom and McIntosh, 1966), *Diplodocus* (Osborn,

1899, 1904; Hatcher, 1901;), *Barosaurus* (Lull, 1919; McIntosh, 2005), *Apatosaurus* (Gilmore, 1936), *Brachiosaurus* (Riggs, 1903) or *Giraffatitan* (Janensch, 1950). In the Iberian Upper Jurassic record, this type of pleurocoels is present in *Lourinhasaurus* (Mocho et al., 2014a), *Dinheirosaurus* (Mannion et al., 2012), *Galveosaurus* (Barco, 2009) and *Lusotitan* (Mannion et al., 2013). This condition is different of the less complex pleurocoels of *Losillasaurus* (Casanovas et al., 2001) or *Turiasaurus* (Royo-Torres et al., 2006).

The presence of a polycamerate textures is also an important feature in several neosauropods (Wedel, 2000, 2003) such as *Apatosaurus* or *Diplodocus* (Wedel, 2000; 2003) and in *Lourinhasaurus* or *Camarasaurus* (camerate to polycamerate, Wedel, 2003; Mocho et al., 2014a). Other important feature in this dorsal vertebra is the presence of a "bifurcated spol", or a lateral and medial spol. The presence of med. spol is observed in diplodocoids (excluding dicraeosaurids), *Brachiosaurus*, *Giraffatitan* and *Mamenchisaurus* (Carballido and Sander, 2014). *Galveosaurus* also presents an incipient med. spol (Barco, 2009; pers. observ., PM), however this condition is not present in *Turiasaurus* (Royo-Torres, 2006) or *Losillasaurus* (Casanovas et al., 2001). The state in *Lusotitan*, *Lourinhasaurus*, *Aragosaurus* is unknown (Mannion et al., 2013; Mocho et al., 2014a; Royo-Torres et al., 2014). *Dinheirosaurus* is not fully prepared and it is not possible to test the presence of a lat. and med. spol in this taxon.

The anterior face of this vertebra is not complete, but the preserved portion suggests an amphicoleous condition. The presence of opisthocoelous dorsal vertebrae up to the sacrum is considered a synapomorphy of Camarasauromorpha (e.g. Salgado et al., 1997; Upchurch et al., 2004) shared by a few Chinese eusauropod taxa such as *Mamenchisaurus* (Young, 1954; Young and Zhao, 1972; Ouyang and Ye, 2002) and *Bellusaurus* (Dong, 1990). The presence of an amphicoelous condition excludes this vertebra from Camarasauromorpha. The presence of polycamerate vertebra, lat. spol and med. spol and amphicoelous dorsal vertebra is a character combination only observed in diplodocids.

The preserved middle caudal vertebra bears some features that allow proposing a more precise systematic approach. The presence of a longitudinal ventral hollow on anterior and middle caudal vertebrae have been proposed as synapomorphy of Diplodocinae (e.g. Wilson, 2002; Carballido et al., 2011) as well as for Titanosaria (e.g. Wilson, 2002; D'Emic, 2012). Nevertheless, this feature present an uncertain distribution within Titanosauria, or inclusively, within Titanosauriformes (depending on the phylogenetic approach) with the presence of this feature in some Chinese somphospondylians such as *Daxiatitan*, *Huanghetitan liujiaxiaensis* You et al. (2006) and *H. ruyangensis* Lü et al. (2007) (placed within Titanosauria by Mannion et al., 2013). The presence of a quadrangular cross-section was also considered a synapomorphy of Diplodocinae (Wilson, 2002; Carballido et al., 2011; Whitlock, 2011 restricted this feature only for anterior caudal vertebrae: character #136) and allow us to relate this vertebra to this clade. The flat posterior articulation also distinguished this caudal vertebra from the procoelous middle caudal vertebrae of lithostrotian titanosaurs (e.g. Gomani, 2005; Powell, 1992; Salgado et al., 1997; Sanz et al., 1999). The general morphology is indistinguishable from middle and posterior caudal vertebrae of the diplodocines *Diplodocus*, *Barosaurus* and *Tornieria* (Hatcher, 1901; Lull, 1919; McIntosh, 2005; Remes, 2006). The presence of fossae (or pleurocoels) in the lateral face of middle caudal vertebra are only recorded in the Morrison and Tendaguru diplodocines (Osborn, 1899, 1904; McIntosh, 2005; Lucas et al., 2006; Remes, 2006). In this specimen, is also observed a more located perforation as occur in other diplodocines such as *Diplodocus* (Hatcher, 1901; Lucas et al., 2006) or *Barosaurus* (McIntosh, 2005). The presence of lateral fossae, ventral hollow and quadrangular cross-section relate MG 30389 caudal vertebra to Diplodocinae clade.

Finally, the preserved ischium bears a lateral tuberosity bordered by a groove. D'Emic (2012, character #106) considered a synapomorphy of Titanosauriformes the presence of raised tubercle without an associated groove. The presence of this groove in the ischium of Batalha

excludes this Portuguese specimen from Titanosauriformes. The observed features in the preserved dorsal vertebra remains, in the caudal centrum and in the ischium agree with the possibility of this set of material belonging to the same taxon or even to the same individual.

7.5.3. Fonte de Oleiro material

Material: Posterior caudal vertebra (MMPM.P/554).

Locality and horizon: Fonte de Oleiro (north of Porto de Mós), Alcobaça Formation, Kimmeridgian-basal Tithonian in age (Manuppella et al., 2000).

Description: The specimen is an incomplete posterior caudal vertebra lacking part of the neural arch (Fig. 7.6). The centrum is cylindrical with subcircular articulations. This vertebra presents an amphicoelous condition, i.e. concave anterior and posterior faces. The ventral face is transversely convex. The articulations for the chevrons have a semicircular outline. On the ventral and lateral face near the articulations, there is a longitudinal striation. The neural arch is located at midpoint of the dorsal surface of the centrum.

Figure 7.6. Posterior caudal vertebra (MMPM.P/554) from Fonte do Oleiro (Porto de Mós) in (a) left, (b) right, (c) ventral, (d) dorsal, (e) anterior and (f) posterior views. Scale bar: 5cm.

Discussion: It has none of the diagnostic features of the groups recognized in Eusauropoda clade so this posterior caudal vertebra should be considered as an indeterminate sauropod.

7.6. CALDAS DA RAINHA, ALCABAÇA AND BOMBARRAL REGION

The following specimens were collected in Imaginário (Caldas da Rainha) and in São Martinho do Porto (Alcobaça). East from the Caldas Diapir there is a wide sector of outcropping Upper Jurassic sediments in the Bombarral Sub-basin. This area corresponds to the Bombarral-Alcobaça Sub-basin *sensu* Taylor et al. (2013). In addition to the new occurrence from Imaginário described herein, in this region there are some classical occurrences referred to Sauropoda in Salir de Matos and São Gregório da Fanadia (Lapparent and Zbyszewski, 1957). A sector of the Bombarral Sub-basin (part of Consolação Sub-basin *sensu* Taylor et al., 2013) is located west from the Caldas Diapir, where is found an Upper Jurassic sequence on the coastal cliffs from Foz do Arelho up to Nazaré (e.g. Hill, 1988; Kullberg et al., 2006). This sector includes localities such as Foz do Arelho, Serra do Bouro and Salir do Porto (Caldas da Rainha) and São Martinho do Porto (Alcobaça). Montejunto, Alcobaça and Bombarral Formations outcrop along this sequence (e.g. Azerêdo et al., 2010). From this sector of the Bombarral Sub-basin some sauropod occurrences were recorded, including axial elements (Lapparent and Zbyszewski, 1957) and several heart-shaped teeth tentatively related with Turiasauria (Royo-Torres et al., 2006, 2009; Mocho et al., 2012, in press; Royo-Torres and Upchurch, 2012).

7.6.1. Imaginário material

Material: Left astragalus (MMPM.P/75).

Locality and horizon: Found by Francisco Jorge Furriel in Imaginário locality (Caldas da Rainha), Bombarral Formation dated to upper Kimmeridgian-Tithonian (Manuppella et al., 1999, 2000; Kullberg et al., 2006; Azerêdo et al., 2010).

Description: An almost complete left astragalus (Fig. 7.7), on which only the posterior edge of the fibular articulation surface is broken. The astragalus is wedge-shaped and transversely longer than proximodistally (more than 50%). The astragalar ascending process extends almost to the posterior margin of the astragalus. Its proximal surface is flat and subhorizontal. The posterior astragalar fossa is not fully prepared, but is possible to recognize the presence of a proximodistal crest, which links the posterior margin of the astragalus with the posteromedial border of the ascending process. This crest subdivides the posterior astragalar fossa. The ventral sector of this crest ends in an unpronounced round boss. The tibial articulation surface is rough, flat-to-concave anteroposteriorly, sloping posteriorly. In proximal view, the lateral part of the posterior edge is convex and the medial part is slightly concave. The medial part of the posterior edge converges medially to the anterior edge of the astragalus, and bears a straight profile. The ventral face is convex anteroposterior and transversely.

Discussion: A divided posterior astragalar fossa, as in MMPM.P/75, is common in sauropods (e.g. Wilson, 2002; Carballido and Sander, 2014). Nevertheless, some titanosaurs reverse this condition to an undivided astragalar fossa (Wilson, 2002). An astragalar ascending process extending to the posterior margin of astragalus was considered a synapomorphy of Neosauropoda (Wilson and Sereno, 1998), *Jobaria*+Neosauropoda (Wilson, 2002) or *Mamenchisaurus*+Neosauropoda (Carballido et al, 2011, *Jobaria* is considered a basal diplodocoid). From the Iberian Upper Jurassic, only *Lourinhasaurus*, *Lusotitan* and *Turiasaurus* preserve the astragalus (Lapparent and Zbyszewski, 1957; Royo-Torres et al., 2006; Mannion et al., 2013; Mocho et al., 2014a). In *Lourinhasaurus*, the ascending process is not preserved (Mocho et al., 2014a), but in *Lusotitan atalaiensis* the astragalar ascending process reaches the posterior margin of the astragalus

(Mannion et al., 2013). In *Turiasaurus riodevensis*, the ascending process occupies a more anterior position being considered by Royo-Torres et al. (2006) as the primitive condition, similar to the condition observed in other basal eusauropods such as *Shunosaurus* or *Omeisaurus*. Fibular facet of the astragalus facing posterolaterally (the anterior border of the fibular articulation is visible in posterior view) were considered by Whitlock (2011) a synapomorphy of Diplodocoidea. The anterior edge of the fibular articulation is visible in posterior view in MMPM.P/75, nevertheless, this results from the fact that the posterior border of this articulation is broken. In MMPM.P/75, the fibular articulation faces laterally. The posterior position of the ascending process was considered as a neosauropod synapomorphy but is also present in some basal eusauropods. According with this, this sauropod might correspond a eusauropod form, being considered herein as an indeterminate eusauropod.

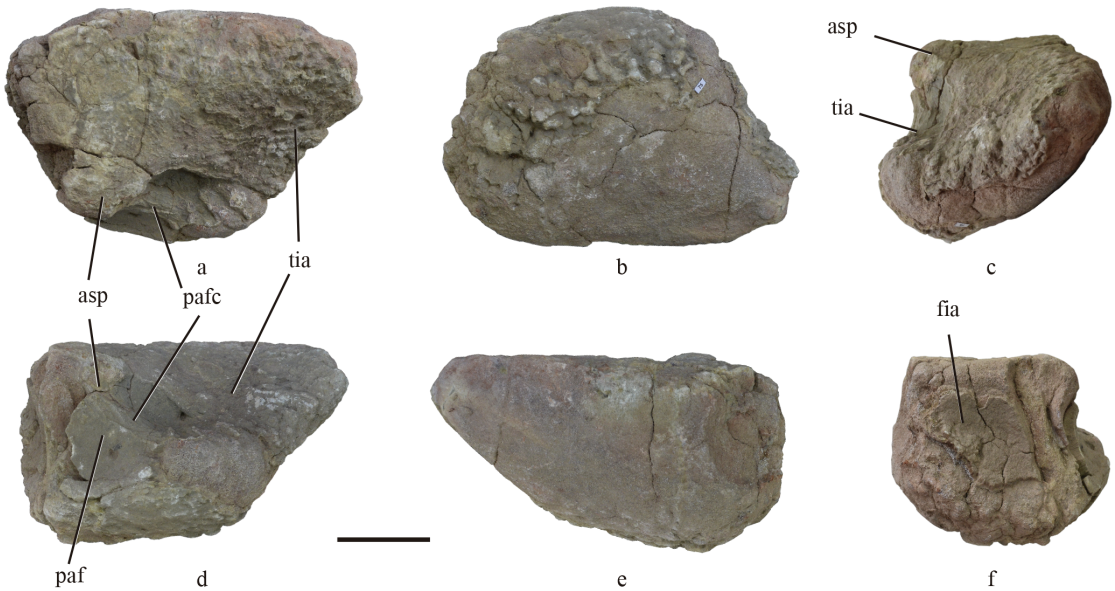

Figure 7.7. Left astragalus (MMPM.P/75) from Imaginário (Caldas da Rainha) in (a) dorsal, (b) ventral, (c) medial, (d) posterior, (e) anterior and (f) lateral views. Scale bar: 10cm. See Anatomical abbreviations for abbreviations.

7.6.2. São Martinho do Porto material

Material: Middle caudal vertebra and a partial anterior or middle chevron (MMPM.P/551). The association of these elements is unknown.

Locality and horizon: Found by Victor Manuel Andrade da Fonseca Lopes in São Martinho do Porto (Alcobaça municipality), probably from the Alcobaça Formation, upper Kimmeridgian-basal Tithonian (Camarate França and Zbyszewski, 1963; Kullberg et al., 2006).

Description: A middle caudal vertebra lacking the neural arch is preserved (Fig. 7.8a-e). This vertebra is dorsoventrally compressed in anterior and posterior view. The centrum is amphicoelous. The posterior face is less concave than the anterior one. The ventral face is convex-to-flat without longitudinal crests. The posterior articulations for the chevrons are subcircular and more developed than the anterior ones with a semi-elliptical outline. The neural arch is clearly displaced to the anterior half of the centrum. A chevron distal end is preserved (Fig. 7.8f-g), probably from a chevron placed next to the transition between the anterior and middle ones. This chevron bears a slight posterior deflection in lateral view and a transversely compressed distal end.

Figure 7.8. Sauropod material (MMPM.P/551) near São Martinho do Porto locality (Alcobaça). Middle caudal vertebra in (a) anterior, (b) posterior, (c) right, (d) dorsal and (e) ventral views. Anterior or middle chevron distal end in right (f) and posterior (g) views. Scale bar: 5 cm. See Anatomical abbreviations for abbreviations.

Discussion: MMPM.P/551 is dorsoventrally compressed as in the caudal vertebrae in *Lusotitan atalaiensis* and in several other basal titanosauriforms (Janensch, 1950; Tidwell et al., 1999, 2001; Upchurch et al., 2004; Canudo et al., 2008; Royo-Torres, 2009), and in *Galveosaurus* (Barco, 2009). Nevertheless, some non-neosauropods also present dorsoventrally compressed caudal centra such as *Cetiosaurus oxoniensis* Phillips (1871) (Upchurch and Martin, 2003). MMPM.P/551 also presents a marked anterior displacement of the neural arch as occur in Titanosauriformes (Salgado et al., 1997; D'Emic, 2012; Mannion et al., 2013) and as in the non-neosauropod eusauropod *Cetiosaurus oxoniensis* (Upchurch and Martin, 2003). The combination of features of MMPM.P/551 is typical but not exclusive of Titanosauriformes, due to the presence of convergences with some eusauropod forms (e.g. *Cetiosaurus*). Nevertheless, this combination is exclusive for these eusauropod forms and Titanosauriformes.

7.7. SAUROPOD FAUNAS OF THE NORTHERN AND CENTRAL SECTOR OF THE BOMBARRAL SUB-BASIN

Most of the information about vertebrate faunas from the Upper Jurassic of the Lusitanian Basin comes from the Turcifal and southern sector of the Bombarral Sub-basins (e.g. Sauvage, 1897-98; Lapparent and Zbyszewski, 1957; Dantas, 1990; Antunes and Mateus, 2003; Mateus, 2006; Ortega et al., 2006, 2009, 2013). Even though the reference of some specimens coming from the central and northern sector of the Bombarral Sub-basin (Sauvage, 1897-98; Lapparent and Zbyszewski, 1957), only in the last half of the 20th century new discoveries start to improve our knowledge about the vertebrate faunas of this sector (e.g. Pérez-Moreno et al., 1999; Rauhut, 2000; Escaso et al., 2007; Malafaia et al., 2010; Caldwell et al., 2015). Some of the classical references for the Upper Jurassic of this region (Sauvage, 1897-98; Lapparent and Zbyszewski, 1957) are

under revision and involve references to sauropods. Those remains were found in Albergaria dos Doze (Pombal municipality); São Martinho do Porto and Fervença (Alcobaça); Salir de Matos, Foz do Arelho and São Gregório da Fanadia (Caldas da Rainha); and Ourém (Vila Nova de Ourém). Part of this material are too fragmentary for a precise systematic approach, highlighting the São Gergório da Fanadia specimens that might represent indeterminate diplodocines (under study), three teeth found in São Martinho do Porto, Ourém and Fervença related to Turiasauria (Royo-Torres, 2009; Mocho et al., 2012, in press; Royo-Torres and Upchurch, 2012) and a tooth from Ourém (Lapparent and Zbyszewski, 1957) probably related to Titanosauriformes.

Other material related to Sauropoda clade was identified in other two fossil sites, the Guimarota mine and the Andrés locality (e.g. Rauhut, 2000; Malafaia et al., 2010). In the Guimarota mine were found some teeth related to Brachiosauridae (Thulborn, 1973; Rauhut, 2000, 2001). From Andrés it were recovered several teeth and postcranial elements, some of them related to a juvenile individual (Malafaia et al., 2010). In this fossil locality were identified Titanosauriformes, Diplodocoidea and Turiasauria remains (Malafaia et al., 2010). More teeth related to Turiasauria, were also reported in the area located east of Caldas Diapir, in São Martinho do Porto and Salir do Porto (Mocho et al., 2012, in press).

This study reports new sauropod occurrences in the north sector of the Lusitanian Basin in order to improve the comprehension of its paleobiodiversity. One of the most interesting specimens is housed in the Muséum national d'Histoire naturelle (Paris), and was collected in Vermoil (Pombal). The study of this dorsal neural spine suggests the presence in this locality of an indeterminate eusauropod not related with Diplodocoidea, and different from the known dorsal spine morphology associated to other known taxa of the Iberian Peninsula, such as *Lourinhasaurus*, *Turiasaurus*, *Losillasaurus* and *Galveosaurus* (dorsal neural spines from *Aragosaurus*, *Zby* and *Lusotitan* are unknown).

In the region of Batalha-Porto de Mós, three specimens are reported. A partial caudal series from the Abadia locality (Leiria) were related to an indeterminate sauropod, showing some particular features that are described for the first time in the Iberian Upper Jurassic record: *i*) the apex of the caudal ribs posteriorly oriented as in *Tastavinsaurus*; and *ii*) the anterior face becomes progressively more flatter than the posterior one along the series, distinct of the condition observed in caudal vertebrae of *Lusotitan*, *Aragosaurus* and *Galveosaurus* and not described in Morrison or Tendaguru sauropods (e.g. Osborn, 1899, 1904; Hatcher, 1901, 1903; Riggs, 1903; Gilmore, 1925, 1936; Lull, 1919; Osborn and Mook, 1921; Janensch, 1950; McIntosch and Williams, 1988; McIntosh et al., 1996a, 1996b; Bonaparte et al., 2000). Despite the presence of these uncommon features, the specimen is too incomplete to obtain a more precise systematic approach.

MG 30389 is a set of elements that might represent a unique individual. A systematic evaluation suggests it belongs to a diplodocine member, in accordance with some occurrences found in Caldas da Rainha (MG 4819, 4821, 4826). Appart from the attribution of the Moinho do Carmo (Alenquer) sauropod to the genus *Apatosaurus* by Lapparent and Zbyszewski (1957), now *Lourinhasaurus alenquerensis* (Dantas et al., 1998) and related to Camarasauridae (Mocho et al., 2014a); the presence of diplodocids in the Upper Jurassic of the Lusitanian Basin have been suggested after the establishment of *Dinheirosaurus lourinhanensis* found in the southern sector of the Bombarral Sub-basin (in Lourinhã, Dantas et al., 1992; Bonaparte and Mateus, 1999). *Dinheirosaurus* was considered as a basal diplodocine (Rauhut et al., 2005; Whitlock, 2011; Mannion et al., 2012; Tschopp and Mateus, 2013; Tschopp et al., 2015). A more derived position for *Dinheirosaurus* within Diplodocinae have been suggested (Mocho et al., 2014b). Furthermore, new specimens from Bombarral and Turcifal Sub-basins were related to Diplodocinae (Mocho et al., 2014b). MG 30389 is a new evidence for the presence of diplodocines in the Portuguese Upper Jurassic, especially in the northern region of the Central Sector of the Lusitanian Basin. This is also supported by the presence of diplodocine caudal vertebrae found in São Gregório da Fanadia (MG 4819, 4821, 4826).

The region east and west of the Caldas Diapir is still a scarcely prospected region of the Bombarral Sub-basin. The identification of several new sites put in evidence the potential of this area. However, so far, the available material only allows to identify an indeterminate eusauropod, and material attributable to member of the Turiasauria group (Mocho et al., 2012, in prep).

The paleobiodiversity found in the central and northern sector of the Bombarral Sub-basin (indeterminate eusauropods, turiasaurs, diplodocines and basal titanosauriforms) is in accordance with the faunistic composition of the southern part of Bombarral Sub-basin and Turcifal and Arruda Sub-basins with diplodocids (including diplodocine forms), camarasaurids (e.g. *Lourinhasaurus alenquerensis*), basal titanosauriforms (*Lusotitan* were recently considered as basal macronarian, brachiosaurid with doubt) and turiasaurs (Dantas et al., 1998; Bonaparte and Mateus, 1999; Antunes and Mateus, 2003; Royo-Torres et al., 2006, 2009; Mannion et al., 2012, 2013; Mateus et a., 2014; Mocho et al., 2012, 2013, 2014a, b; Royo-Torres and Upchurch, 2012). This paleobiodiversity is also in accordance with the sauropod faunas recorded in the Tithonian-Berriasian sediments of the Villar del Arzobisbo Formation from Spain, with turiasaurs (*Losillasaurus* and *Turiasaurus*), basal macronarians (*Aragosaurus*), some diplodocid specimens, and *Galveosaurus* (Sanz et al., 1987; Casanovas et al., 2001; Sánchez-Hernández, 2005; Royo-Torres et al., 2006, 2007, 2009, 2014; Barco, 2009; Gascó, 2010; Royo-Torres and Upchurch, 2012).

7.8. CONCLUSIONS

The north region of the Central Sector of the Lusitanian Basin (central and northern region of Bombarral Sub-basin) is relatively poor in sauropod fossil record. Up today, some classical occurrences and material from Guimarota mine and the Andrés fossil-site were source of a short view about the paleobiodiversity of this group on this sector of the Lusitanian basin. The present work describes and discuses some unpublished occurrences found on the central and north sector of the Bombarral Sub-basin, more precisely, at north of the Maciço Calcário Estremenho and in Upper Jurassic sediments east and west from Caldas Diapir.

The Upper Jurassic of the Lusitanian Basin is relatively scarce in cervical and dorsal vertebrae remains. The description of a middle/posterior dorsal neural spine from Vermoil allow us to identified a dorsal neural spine morphology not described for the Portuguese Upper Jurassic record and relatively different from *Turiasaurus*, *Losillasaurus*, *Dinheirosaurus*, *Lourinhasaurus* and *Galveosaurus* dorsal neural spines. On Pombal area, it is possible to recognize an indeterminate eusauropod and remains related to Turiasauria, Diplodocoidea and Titanosauriformes. The region just to the north from the Maciço Calcário Estremenho, including Batalha, Porto de Mós and Vila Nova de Ourém have yields remains of indeterminate eusauropods, turiasaurs, diplodocines and titanosauriforms. On other hand, the Upper Jurassic sequence outcropping east and west from Caldas Diapir bears several occurrences, but only part of these specimens could be related to Eusauropoda, and some of them (heart-shaped teeth) related to the Turiasauria clade. The Guimarota mine, Andrés and Casal Novo localities are some of the most important fossil-sites from the central and the northern sector of the Bombarral Sub-basin. Nevertheless, the new occurrences reported herein put in evidence the potential of this area in vertebrate fossil-sites.

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CHAPTER 8

Turiasauria-like teeth from the Upper Jurassic of the Lusitanian Basin, Portugal

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Turiasauria-like teeth from the Upper Jurassic of the Lusitanian Basin, Portugal

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Turiasauria is a clade of eusauropods with a wide stratigraphic range that could extend from the Bathonian to the lower Aptian including *Turiasaurus*, *Losillasaurus*, *Zby* and putatively, *Galveosaurus*, *Atlasaurus* and isolated remains from Middle Jurassic-to-Lower Cretaceous. Some are characterised by the presence of heart-shaped teeth. Several tooth occurrences from the Portuguese Upper Jurassic with this type of morphology (SI: 1.1–1.8) are reported and discussed. If this morphology is regarded as synapomorphic of Turiasauria, the teeth will be tentatively related to this clade. From a sample of 43 teeth, three main morphotypes are described. Three hypotheses might explain the morphological variation: (1) the range of tooth morphologies indicates variation in the jaw, (2) the range of tooth morphologies indicates taxonomic variation or (3) a combination of both. The general wear pattern in morphotypes I and II starts with a distal facet, then the appearance of mesial/apical facet and finally a 'V'-shaped facet. In morphotype III, the wear begins with a mesial facet. The variability observed for Portuguese Upper Jurassic specimens is congruent with the morphological variability along the tooth row shown by other sauropods with spatulate/spoon-shaped teeth and it is considered the most parsimonious hypothesis to explain it.

Keywords: Sauropoda; Eusauropoda; Turiasauria; Upper Jurassic; Lusitanian Basin; Teeth

Introduction

The sauropods are one of the vertebrate groups better represented in the last part of the Portuguese Upper Jurassic of the Lusitanian Basin (Kimmeridgian-Tithonian). Their study improves the understanding of vertebrate faunas and their paleobiogeography in this period. Recent works suggest that Iberian sauropods are represented by endemic genera (Dantas et al. 1998; Bonaparte and Mateus 1999; Casanovas et al. 2001; Antunes and Mateus 2003; Sánchez-Hernández 2005; Royo-Torres et al. 2006; Mateus et al. 2014) closely related to groups well represented in other continents during the Upper Jurassic like brachiosaurids (Antunes and Mateus 2003; Mannion et al. 2013), diplodocids (Bonaparte and Mateus 1999; Mannion et al. 2012; Mocho, Royo-Torres, Malafaia, et al. 2014) or camarasaurids (Mocho, Royo-Torres, et al. 2014). The supposed close relationship of the Portuguese sauropods with taxa from the North American Upper Jurassic of the Morrison Formation (e.g. Lapparent and Zbyszewski 1957) is less close than it is interpreted in other dinosaur groups. In fact, there are references to genera and even species of theropods, ornithopods and stegosaurs with an amphiatlantic distribution (Galton 1980; Mohr 1989; Pérez-Moreno et al. 1999; Martin 2000; Mateus and Antunes 2000a; Mateus and Antunes 2000b; Ortega et al. 2006; Mateus et al. 2006; Escaso et al. 2007; Malafaia et al. 2007, 2010, In press; Ortega et al. 2009; Escaso et al. 2010).

This study analyses a sample of 43 sauropod teeth collected in several Upper Jurassic localities of the Lusitanian Basin. They are tentatively assigned to Turiasauria, a basal eusauropod clade, based on its heart-shaped morphology. The meaning of three distinct morphotypes is also discussed. Several other heart-shaped teeth from Europe and Africa are also compared with the present sample. The information provided allows to propose a stratigraphic range for this tooth morphology in the Iberian Upper Jurassic wider than was previously thought.

Turiasauria clade

Currently, in the Iberia Peninsula, there are eight sauropod species ranging from Kimmeridgian to lower Berriasian: *Aragosaurus ischiaticus* Sanz et al. 1987; *Lourinhasaurus alenquerensis* (Lapparent and Zbyszewski 1957); *Dinheirosaurus lourinhanensis* Bonaparte and Mateus 1999; *Lusotitan atalaiensis* (Lapparent and Zbyszewski 1957); *Galveosaurus herreroi* Sánchez-Hernández 2005; *Losilla-*

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saurus giganteus Casanovas et al. 2001; *Turiasaurus riodevensis* Royo-Torres et al. 2006; and *Zby atlanticus* Mateus et al. 2014.

Turiasauria is defined as a stem-based taxon including all eusauropods more closely related to *T. riodevensis* than to *Saltasaurus loricatus* Bonaparte and Powel 1980 (Royo-Torres et al. 2006). Therefore, it includes *Turiasaurus*, *Losillasaurus*, *Zby*, '*Neosodon*', '*Cardiodon*' and putatively *Galveosaurus* (Royo-Torres et al. 2006, 2009; Royo-Torres and Cobos 2009; Royo-Torres and Upchurch 2012; Mateus et al. 2014) and *Atlasaurus* (Royo-Torres, Cobos, et al. 2014; Xing et al. 2015). The inclusion in Turiasauria of three Spanish sauropods from the Villar del Arzobispo Formation: *Turiasaurus*, *Losillasaurus* (Tithonian-lower Berriasian) and *Galveosaurus* (Tithonian-lower Berriasian) is based on some phylogenetic hypotheses (Royo-Torres et al. 2006, 2009, 2012; Royo-Torres, Upchurch, et al. 2014; Royo-Torres and Upchurch 2012; Carballido and Sander 2014; Mocho, Royo-Torres, et al. 2014). *Galveosaurus* has been considered in different phylogenetic positions along its history. It was considered as a cetiosaurid (Sánchez-Hernández 2005), a basal eusauropod (Canudo et al. 2006), after it was proposed as a possible neosauropod (Barco et al. 2005), suggesting first its inclusion in Diplodocoidea (Barco 2005) and later in Macronaria? (Barco et al. 2006). *Galveosaurus* was also considered as a non-titanosauriform macronarian (Barco 2009; Barco et al. 2009; Carballido et al. 2011; Carballido and Sander 2014; Mannion et al. 2013). D'Emic (2012) noted the possibility that the holotype material of *Galveosaurus* might represent more than one individual. For this author, the presence of an elongate cervical vertebra and middle caudal vertebrae with anteriorly set neural arches might relate *Galveosaurus* to Titanosauriformes. The presence of a rounded proximolateral corner of the humeri suggested affinities to Brachiosauridae (D'Emic 2012), but this feature is also present in basal eusauropods, in particularly, in turiasaurs (e.g. Casanovas et al. 2001; Royo-Torres et al. 2006, 2009; Royo-Torres and Upchurch 2012). The discovery of more material and an accurate systematic revision will be important to obtain a more precise phylogenetic approach for this taxon.

More recently, the presence of more turiasaurian occurrences in Spain, Portugal, France, the UK, Tanzania and Morocco has been suggested (Mateus 2009; Royo-Torres et al. 2009; Royo-Torres and Cobos 2009; Santos et al. 2009; Ortega et al. 2010; Cobos et al. 2011; Mocho et al. 2012; Royo-Torres and Upchurch 2012; Mateus et al. 2014; Royo-Torres, Cobos, et al. 2014; Suñer et al. 2014; Xing et al. 2015). From Spain, an unnamed specimen from Riodeva (Teruel) with postcranial material (Royo-Torres et al. 2009) and an isolated caudal vertebra from Veguillas de la Sierra (Teruel) were related to Turiasauria (Royo-Torres et al. 2008). Both specimens come from the Villar del Arzobispo Formation, considered as Tithonian-lower Berriasian in age (Mas et al. 1984, 2004). Also, Canudo et al. (2010) refer to cf. *Turiasaurus riodevensis* a fragment of a dentary with some teeth from the Kimmeridgian of Asturias (Spain).

The first evidence of turiasaurian remains in the Lusitanian Basin was based on an isolated tooth (Royo-Torres et al. 2006, 2009) from Alcobaça Formation (Kimmeridgian). Subsequently, Mateus (2009) referred to *Turiasaurus riodevensis*, an incomplete specimen composed by an almost complete hindlimb associated with a scapula, a coracoid, a tooth and a middle chevron, collected in Vale de Pombas (ML 368). This specimen was firstly related to *Camarasaurus* (Mateus 2005), but a recently systematic revision established a new genus and species, *Zby atlanticus*, which was tentatively placed within Turiasauria as a closely related form to *Turiasaurus riodevensis* (Mateus et al. 2014). Ortega et al. (2010) assigned to *Turiasaurus* some teeth collected on the region of Torres Vedras (Portugal) from the upper Kimmeridgian-Tithonian sediments of the Freixial Fm. and Praia de Amoreira-Porto Novo Fm. Santos et al. (2009) described a new ichnospecies (*Polyonyx gomesi* Santos et al. 2009) in the Galinha tracksite from the Middle Jurassic of the Maciço Calcário Estremenho (Portugal) that they related to a basal eusauropod, probably a form within the Turiasauria clade. If these footprints belong to Turiasauria, they would be, for now, one of the most ancient occurrences for this clade, together with some teeth from the UK (see Royo-Torres and Upchurch 2012). This ichnospecies might also be present in the Villar del Arzobispo Fm. So far, no trackway has been described, but some isolated manus and pes has been related with *Polyonyx* (Cobos et al. 2008; Royo-Torres 2009; Santos et al. 2009) in two sites from the El Castellar locality in Teruel (Spain).

Several teeth collected in the Middle and Upper Jurassic of UK and in the Upper Jurassic of France were also related to Turiasauria due the similarities shared with the Iberian heart-shaped teeth (Royo-Torres et al. 2006, 2009, Royo-Torres, Cobos, et al. 2014; Royo-Torres and Upchurch 2012), particularly the teeth of '*Neosodon*' (Moussaye de la 1885; Buffetaut and Martín 1993) and '*Cardiodon rugolusus*' Owen 1841 (Owen 1841, 1844, 1875), three Middle Jurassic teeth from Peterborough (the UK) assigned to '*Cetiosauriscus leedsi*' (NHMUK R3377, Hulke 1887) and five teeth from the Upper Jurassic of Aylesbury (the UK) previously assigned to '*Hoplosaurus*' and '*Pelorosaurus*' (one numbered NHMUK R2004–5 and three numbered NHMUK R2565; Lydekker 1893; Woodward 1895).

More recently, the reassessment of some Gondwanan sauropods from Tendaguru Formation (Tithonian) in Tanzania could provide evidence for the presence of Turiasauria in Gondwana during the Upper Jurassic, suggesting a wider paleobiogeographic range than previously thought. Royo-Torres and Cobos (2009) and

Royo-Torres, Cobos, et al. (2014) related to Turiasauria a complete right manus (HMN MB.R.2093.1-12), a partial caudal series described by Bonaparte et al. (2000, HMN MB.R.2091.1-30), an astragalus (HMN MB.R.2095.6) and a humerus (HMN MB.R.2910). Royo-Torres, Cobos, et al. (2014) and Xing et al. (2015) also suggested the placement of *Atlasaurus* from the Middle Jurassic (Bathonian-Callovian) of Morocco inside Turiasauria.

Geological settings

The described teeth were mainly collected northwestern of Lisbon, along the coastal cliffs between the localities of Cambelas and Praia da Gralha in Torres Vedras, Lourinhã, Caldas da Rainha, Alcobaça and Peniche municipalities (Figure 1). In this area, outcrops an Upper Jurassic to Lower Cretaceous sedimentary sequence, deposited in the Lusitanian Basin. The Upper Jurassic beds are dated from middle Oxfordian to the base of Cretaceous (Schneider et al. 2009), and represent a third rifting episode (Rasmussen et al. 1998, Kullberg et al. 2006) marked by an internal differentiation resulting in the formation of several sub-basins (Turcifal, Arruda and Bombarral sub-basins) followed by an important siliciclastic input which progressively filled these sub-basins (Hill 1988; Pena dos Reis et al. 2000; Kullberg et al. 2006). Since the Kimmeridgian, the sedimentary sequence is marked by a strong siliciclastic nature, with a continental signature on

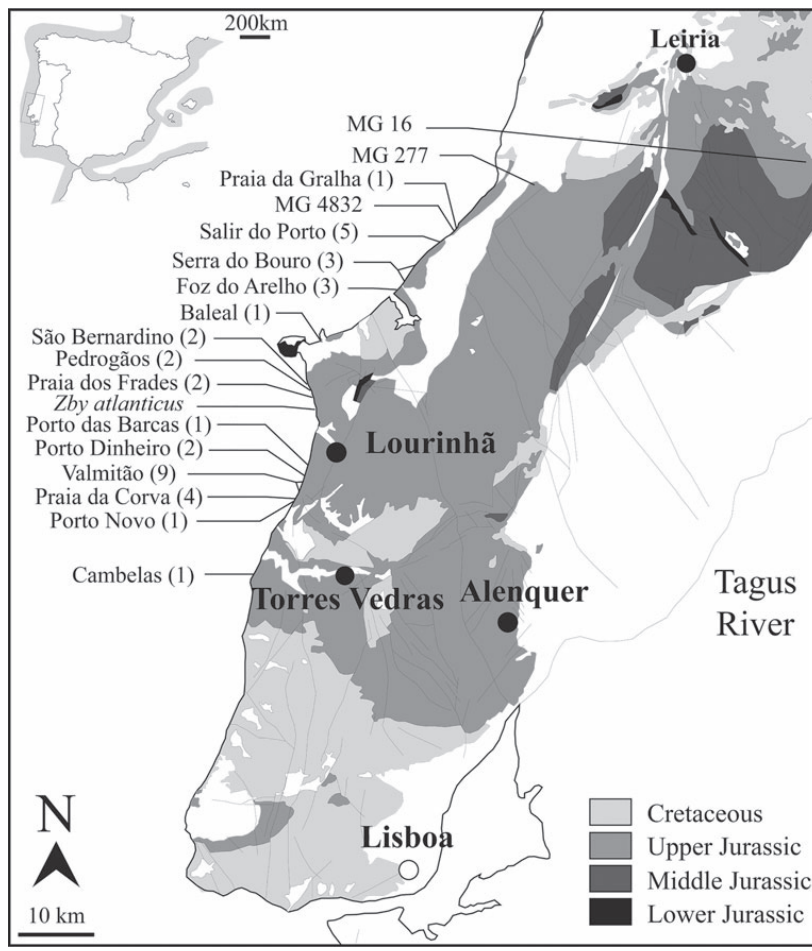

Figure 1. Geological map (adapted from Oliveira et al. 1992) showing the Portuguese Mesozoic levels and the localities from where come the studied heart-shaped teeth. The number in parenthesis is the number of teeth found in each locality.

the top of the sequence corresponding to the last part of the Upper Jurassic (e.g. Hill 1988; Manuppella et al. 1999; Kullberg et al. 2006).

Different stratigraphic approaches have been proposed for the Upper Jurassic sequence of these sub-basins (e.g. Hill 1988; Leinfelder 1993; Manuppella et al. 1999; Kullberg et al. 2006; Schneider et al. 2009; Martinius and Gowland 2011; Taylor et al. 2014; see Figure 2). The teeth described were found in sediments from several Upper Jurassic formations of the Lusitanian Basin, including Montejunto (?), Alcobaça, Praia da Amoreira-Porto Novo, Sobral, Freixial and Bombarral Formations. All of them, except the Montejunto Fm., were included in the Lourinhã Group proposed by Yagüe et al. (2006). One of the first references of this tooth morphology in the Portuguese Upper Jurassic was found near Ourém (MG 16, Sauvage 1897–98), probably from Montejunto Fm. or Alcobaça Fm, upper Oxfordian or Kimmeridgian-basal Tithonian in age, respectively (Mouterde et al. 1979; Manuppella et al. 1999, 2000).

Most of the teeth come from the 'Lourinhã Formation' (unit proposed by Hill 1988), which includes the Praia da Amoreira-Porto Novo (included in the Alcobaça Beds *sensu* Manuppella et al. 1999), Sobral, Freixial and Bombarral Formations (Manuppella et al. 1999) (Figure 2). Figure 2 shows the correspondences among some stratigraphic approaches as well as the stratigraphic position of the teeth analysed here. "Lourinhã Formation" *sensu* Hill (1988) is interpreted as upper Kimmeridgian-to-basal Berriasian in age (Leinfelder 1986; Hill 1988; Leinfelder and Wilson 1989; Mohr 1989; Manuppella et al. 1999). This unity was subdivided in five members by Hill (1988) that in part corresponds to the formations proposed by Manuppella et al. (1999) (see Figure 2). The Sobral Fm. (= Praia Azul member of Lourinhã Fm. *sensu* Hill 1988) is a relatively well-dated unit, upper

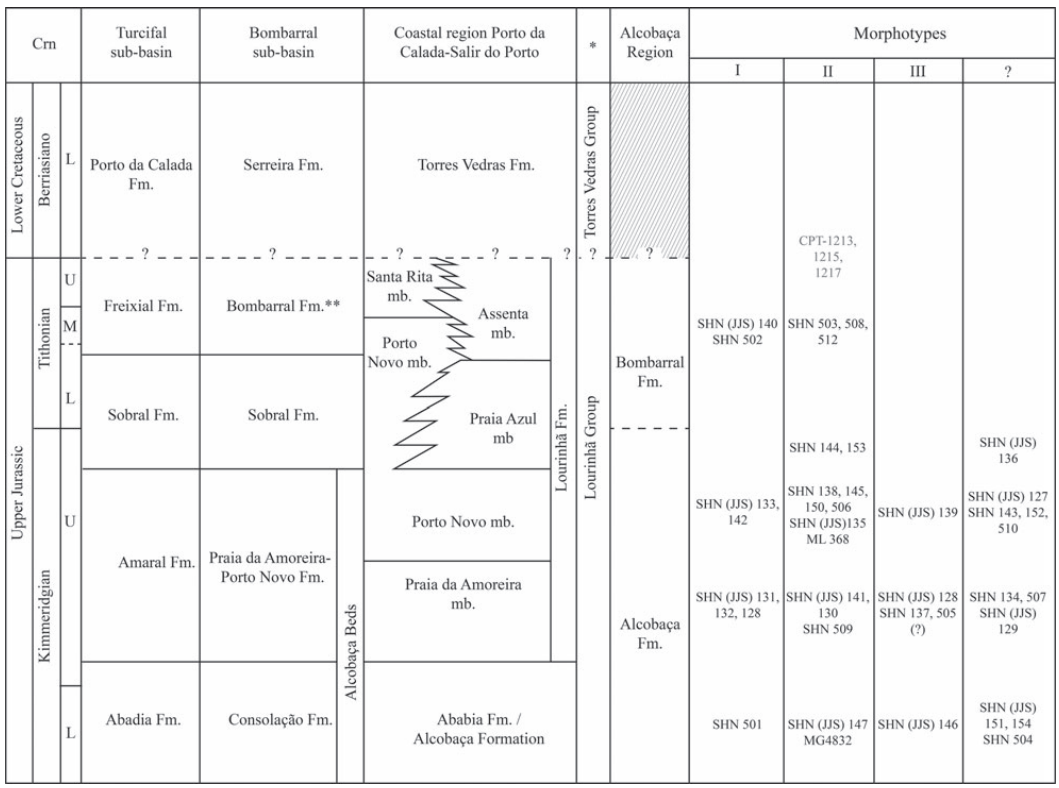

Figure 2. Stratigraphic correlation between the nomenclature proposed for Turcifal sub-basin (based on Pereda-Suberbiola et al. 2005; Kullberg et al. 2006; Schneider et al. 2009), Bombarral sub-basin (based on Manuppella et al. 1999), the coastal sector from Porto da Calada to Salir do Porto (based on Hill 1988) and Alcobaça region (based on Kullberg et al. 2006; Azerêdo et al. 2010), and the respective stratigraphic position of the described teeth by morphotype. Crn, Chronostratigraphy; U, upper; M, middle; L, lower; *sensu Yagüe et al. 2006; **other formations are identified in Lourinhã region by Manuppella et al. 1999 as lateral correlatives of Bombarral Fm.

Kimmeridgian to lower Tithonian in age (Fürsich 1981). It is also important to refer that the coastal sedimentary sequence south of Sizandro river mouth, which corresponds to the transition of Sobral Fm. and Freixial Fm. (Assenta member of Hill 1988), is progressively younger to the south, with a stratigraphic range from lower to upper (?) Tithonian (Leinfelder 1987; Hill 1988; Schneider et al. 2009). Some teeth were found in the coastal cliffs of Salir do Porto and São Martinho do Porto and in Fervença locality where outcrops the Alcobaça Fm. (*sensu* Camarate França and Zbyszewski 1963; Azerêdo et al. 2010). The Alcobaça Fm. in Salir do Porto was dated to the lower Kimmeridgian (Schneider et al. 2009). Considering the inclination of strata and the present cartographic data, it is reasonable to consider a younger age to Serra do Bouro outcrops, probably middle (?) Kimmeridgian to Tithonian, where Alcobaça Fm. transits to the Bombarral Fm., near Boavista do Bouro locality (Camarate França and Zbyszewski 1963; Azerêdo et al. 2010). The Tithonian Bombarral Fm. is on the top of the upper Kimmeridgian-to-lower Tithonian Sobral Fm. in Bombarral and Turcifal sub-basins (Manuppella et al. 1999). Summarising, all the analysing heart-shaped teeth from Portugal are recorded from the upper Oxfordian (?) to the lower-to-upper Tithonian on the Upper Jurassic of the Lusitanian Basin.

Anatomical abbreviations

Awf, apical wear facet; bwf, wear facet at the base of the crown; cwf, carina wear facet; lag, labial groove; lic, lingual crest; SI, slenderness index, "v" wf, "V"-shaped wear facet.

Institutional abbreviations

BHN, Muséum d'Histoire Naturelle de Boulogne-sur-Mer, Boulogne-sur-Mer, France; FCPT-D, Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain (plus CPT for the fossil material deposited in the museum [Museo Aragonés de Paleontología]); HMN, Humboldt Museum für Naturkunde, Berlin, Germany; MG, Museu Geológico do Laboratório Nacional de Energia e Geologia, Lisbon, Portugal; ML, Museu da Lourinhã, Lourinhã, Portugal; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MUJA, Museo del Jurásico de Asturias, Asturias, Spain; NHMUK, Natural History Museum, London, UK; SHN, Sociedade de História Natural, Torres Vedras, Portugal (plus (JJS) for the José Joaquim collection deposited in the Sociedade de História Natural).

Systematic Paleontology

Dinosauria (Owen 1841); Saurischia (Seeley 1887); Sauropoda (Marsh 1878); Eusauropoda (Upchurch 1995); ?Turiasauria (Royo-Torres et al. 2006)

Material

Forty-three complete and partial preserved teeth: SHN (JJS) 127–133, 135, 136, 139–142, 146–149, 151, 154, 504; SHN 134, 137, 138, 143–145, 150, 152, 153, 501–503, 505–512; MG 16, 277, 4832.(Table 1)

Description of general morphology

Each tooth crown has a heart-shaped spoon-like morphology, compressed labiolingually and presenting an enamel with wrinkled texture. In generally, the crown is slightly apicomesially projected and the teeth reach the maximum mesiodistally width near the base of the apex (the apex is considered herein as the apical portion of the tooth, apical to the sagittal deflection of mesial and distal edge). Excluding the most worn teeth, the slenderness index (SI: crown height/maximum crown breadth; *sensu* Upchurch 1998) ranges between 1.1 and 1.8.

On the labial face, the teeth display an apicobasal bulge bounded by shallow grooves with the same orientation. The lingual face has a low apicobasal ridge, which might extend along the entire apicobasal length. The mesial and distal edges are not parallel and diverge from the base of the tooth. The transition between the row and crown is marked in all the teeth. The teeth exhibit asymmetrical 'D' to lenticular-shaped cross section with a strongly convexity labial face and a flat-to-smooth concave lingual face. The maximum labiolingual width is located near the mesial edge, resulting in steeply angled mesial part on labial surface. The asymmetrical apex deflects distally and could bear mesial, distal and apical wear facets depending of the wear development. The mesial and distal edges of the apex are straight to slightly convex and concave, respectively, in labial/lingual view. Generally, the distal edge of the apex is longer than the mesial one (excluding the morphotype III, see below). Crown-to-crown occlusion produced "V"-shaped wear facets. Some teeth are heavily worn and, in some cases, it is possible to observe the dentine. The wear facets will be commented in detail after the definition and description of the three proposed morphotypes.

The wrinkling pattern of the enamel is similar to those present in several spatulate- or spoon-like teeth (e.g. *Camarasaurus*, *Turiasaurus, "Neosodon"*) marked by an alternation between apicobasal and waved grooves and ridges. Along its length, these ridges join together forming an anastomosed pattern. This pattern is smoother at the tip of the apex probably because of abrasion, like in other sauropod teeth (e.g. *Amygdalodon*, Carballido and Pol 2010).

Definition of the morphotypes

Despite a general morphology shared by every studied tooth, a division into three different morphotypes is

Table 1. Studied heart-shaped teeth from the Portuguese Upper Jurassic (see appendix 1 to measurements).

Locality	Formation*	Age	Wear	Morphotype	**SI**
Valmitão Norte	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Moderate	III or II	1.21
Praia dos Frades	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Absent/weak	III	1.12
Praia de Pedrogãos	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Strong	?	?
Praia de Pedrogãos	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Strong	II	1.12
Praia dos Frades	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Moderate	I	1.54
São Bernardino	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Moderate	I	1.41
Valmitão Norte	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Absent/weak	I	?
Valmitão Norte	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Moderate	II	1.32
Porto das Barcas	Sobral Fm.	Upper Kimmeridgian-lowerTithonian	Moderate	?	?
Praia da Corva	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Moderate	III	1.30
Cambelas	Freixial Fm.	Tithonian	Absent/weak to moderate	I	1.81
Baleal	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Moderate	II	1.39
Praia da Corva	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Absent/weak	I	1.55
Salir do Porto	Alcobaça Fm.	Lower Kimmeridgian	Absent/weak	III	?
Salir do Porto	Alcobaça Fm.	Lower Kimmeridgian	Absent/weak	II	1.43
?	?	?	Moderate	II	1.41
?	?	?	Strong	III	1.06
Salir do Porto	Alcobaça Fm.	Lower Kimmeridgian	Moderate	?	?
Salir do Porto	Alcobaça Fm.	Lower Kimmeridgian	Absent/weak	?	?
Salir do Porto	Alcobaça Fm.	Lower Kimmeridgian	Absent/weak	?	?
Valmitão	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Absent/weak	?	?
São Bernardino	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Absent/weak	III	1.23
Porto Novo	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Absent/weak	II	1.42
Valmitão Norte	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Moderate	?	1.41
Porto Dinheiro	Sobral Fm.	Upper Kimmeridgian-lowerTithonian	Absent/weak	II	1.33
Praia da Corva	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Moderate (?)	II	?
Serra do Bouro	Bombarral Fm.	Tithonian	Moderate	II	?
Serra do Bouro	Bombarral Fm.	Tithonian	Moderate	I or II	1.66
Porto Dinheiro	Sobral Fm.	Upper Kimmeridgian-Tithonian	Absent/weak	II	?
Praia da Gralha	Alcobaça Fm.	Lower Kimmeridgian	Moderate	I	?
Foz do Arelho	Bombarral Fm.	Tithonian	Absent/weak	I	?
Foz do Arelho	Bombarral Fm.	Tithonian	Moderate	II	1.30
Valmitão Sul	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Absent/weak	III(?)	?
Valmitão Norte	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Moderate to strong	II	?
Valmitão Sul	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Moderate	?	?
Serra do Bouro	Bombarral Fm.	Tithonian	Absent/weak	II	1.34
Valmitão Sul	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Absent/weak	II	1.32
Praia da Corva	Praia de Amoreira-Porto Novo Fm.	Upper Kimmeridgian-basal Tithonian	Strong	?	?
?	?	?	?	II	?

(*Continued*)

Table 1 – *continued*

Locality	Formation*	Age	Wear	Morphotype	**SI**
Foz de Arelho	Bombarral Fm.	Tithonian	Absent/weak	II	1.47
São Martinho do Porto	Alcobaça Fm.	Lower Kimmeridgian	Moderate	II	1.48
Fervença		Lower Kimmeridgian	?	?	?
Ourém	Montejunto or Alcobaça Fm.	Middle-to-upper Oxfordian or Kimmeridgian-basal Tithonian	?	?	?

Notes: The stratigraphic information is based on Manuppella et al. (1999), Kullberg et al. (2006) and Azerêdo et al. (2010).

here proposed. Nevertheless, the absence of clear morphological limits between the described morphotypes indicates that these could represent a gradient of morphological variation of the same taxonomic unit (see discussion below). Morphometric analyses were discarded because the original tooth morphology is obliterated in most of the preserved teeth by a significant worn. SHN (JJS) 127, 129, 136, 151, 154 and 504, SHN 134, 143, 152, 507, 510 and MG 16 and 277 could not be assigned to any of the morphotypes due to their preservation state or by the presence of severe worn.

Morphotype I (SHN (JJS) 131, 132, 133, 140, 142; SHN 501, 502, see Figure 3): The heart-shaped crowns are more apicobasally elongated and labiolingually compressed than the morphotypes II and III. They also bear the higher SI values, ranging between 1.8 and 1.6 (teeth with moderate wear have lower SI values, around 1.5–1.4). The labial face is markedly convex mesiodistally and weakly convex apicobasally. The lingual face is concave apicobasally and mesiodistally and the lingual crest can occupy all the apicobasal extension. In this morphotype, mesial and distal edges in the base of crown are closely parallel and straighter than in the

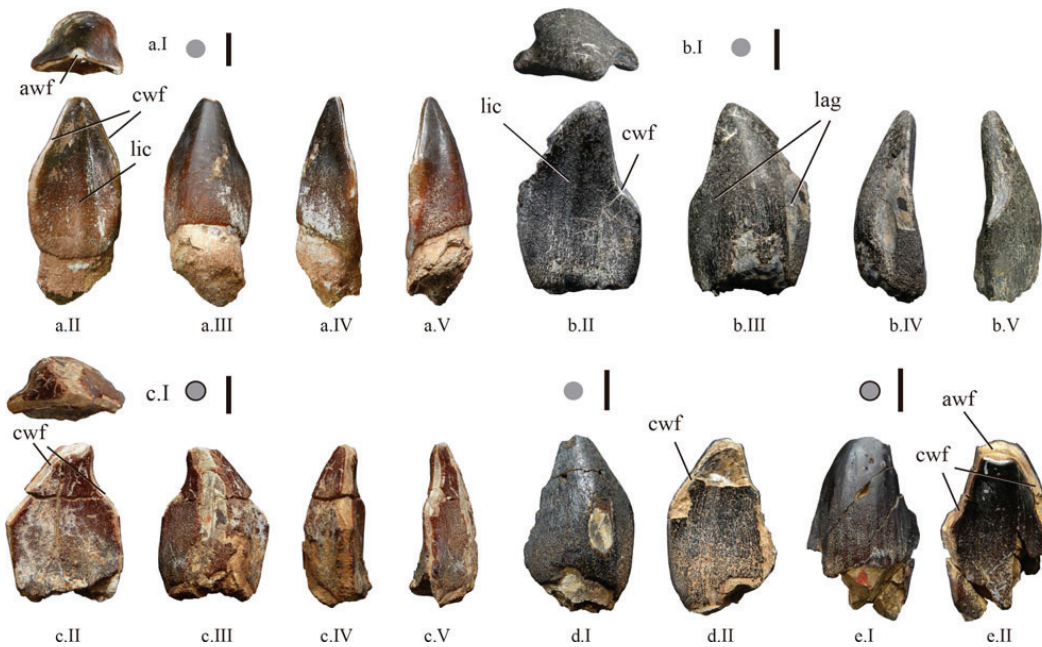

Figure 3. Heart-shaped teeth assigned to the morphotype I. SHN (JJS) 140 in apical (a.I), lingual (a.II), labial (a.III), distal (a.IV) and mesial (a.V) views; SHN (JJS) 142 in apical (b.I), lingual (b.II), labial (b.III), mesial (b.IV) and distal (b.V) views; SHN (JJS) 132 in apical (c.I), lingual (c.II), labial (c.III), mesial (c.IV) and distal (c.V) views; SHN (JJS) 133 in labial (d.I) and lingual (d.II) views; and SHN 501 in labial (e.I) and lingual (e.II) views. Scale bar = 1 cm; grey circle = absent/weak worn; delimited grey circle = moderate worn; black circle = strongly worn.

other two morphotypes. The apex is particularly longer in these teeth. It occupies one half or more than the total crown height (apex/crown height ratio > 0.5). In this morphotype, the apex presents a slight distal deflection, which is not so pronounced as in the morphotype II. The distal edge of the apex is concave and the mesial one is convex-to-straight. Both are criteria for the orientation of these teeth.

Morphotype II (SHN (JJS) 130, 135, 141, 147, 148; SHN 138, 144, 145, 150, 153, 503, 506, 508, 509, 511, 512, see Figure 4*):* It is more abundant in the sample, with a well-defined heart-shaped outline, crown projected apicomesially and a more pronounced curvature of the apex than in the morphotype I. This morphotype bears intermediate SI values, ranging between 1.5 and 1.3 (teeth with moderate or strong wear could reach a SI next to 1.2). The lingual surface is not so concave as the morphotype I. The lingual crest does not reach the base of the crown that develops a flat-to-convex mesiodistal platform. This platform is not so well individualised from the remaining lingual surface by a marked cingulum as that occurs in *Camarasaurus, Mamenchisaurus* or *Euhelopus* tooth (e.g. Suteethorn et al. 2013). Unlike morphotype I, the mesial and the distal edges of the crown are basally convex, resulting from a mesiodistal basal expansion of the crown. The apex is shorter than in morphotype I (apex/crown height ratio ranging between ≈ 0.5 and 0.38).

Morphotype III (SHN (JJS) 128, 139, 146, 149; SHN 137, and SHN 505 with doubt, see Figure 5*)*: This corresponds to heart- to subsquared-shaped teeth more compressed labiolingually and shorter than the other two morphotypes (SI < 1.3). The labial face is not so convex as in morphotypes I and II. The lingual face is concave apicobasally and flat-to-concave mesiodistally with a similar platform at the base of the crown as that occurs in the morphotype II, but less pronounced. The lingual apicobasal crest in this morphotype is incipient-to-absent. On the distal edge, in the transition between the apex and the base of the crown, there is a round shoulder lingually projected resulting from the concavity of the distal edge of the apex. Unlike morphotypes I and II, the distal edge is shorter than the mesial edge. The apex is shorter than in morphotypes I and II (apex/crown height ratio < 0.3). SHN (JJS) 139 (Figure 5(a)) presents a morphology between morphotypes II (SI higher than morphotype III) and III (apex shorter than morphotype II), but it is considered here as morphotype III because of the presence of a short apex.

Wear pattern

The sample presents variable wear patterns. We consider here three main states of wear: (i) absent or weak, without wear facets (e.g. Figure 4(a),(c),(e)), probably non-functional teeth, or teeth with marked mesial wear facets, but sometimes with a slight worn on the distal edge of the apex (e.g. Figures 3(b), 4(d) or 5(c)); (ii) moderate, wear facets in both edges of the apex and an incipient (Figures 3(d) and 4(b)) or well-marked (e.g. Figures 3(c), 4(h), 6(b), 10(d)–(e)) apical wear facet; (iii) strong, the three wear facets are fused in a unique 'V'-shaped wear facet (Figure 6(d),(e),(f)). The wear facet on the distal edge is generally longer and more developed than the mesial one, except in the teeth of morphotype III. As far as can be checked, the wearing in morphotypes I and II begin in the distal edge (Figure 3(b) and 4(d)). In less worn teeth, the distal wear is always present and when the mesial one is also present, the distal one is more developed than the mesial one. In a more advanced wear state (moderate), the distal facet becomes more pronounced and the mesial one becomes well defined. An incipient-to-marked apical wear facet is generally associated with moderately worn teeth (e.g. SHN (JJS) 140 or SHN 508; Figures 3(a) and 4(b)). In more advanced stages of wear (strong wear), the mesial, distal and apical facets produce a unique 'V'-shaped facet (SHN (JJS) 129 or SHN (JJS) 130, Figure 6). The morphotype III teeth show a different condition from the previous morphotypes: the wearing starts in the mesial edge, as in SHN 137 (Figure 5(c)).

Generally, teeth with incipient wear present wear facets with high lingual or labial inclination (almost vertical). More developed wear facets become progressively more subhorizontal (e.g. SHN (JSS) 141). In almost all studied teeth, the wear facets slope lingually, which might suggest a maxillary/premaxillary position (see Nowinski 1971, Calvo 1994, Barrett and Upchurch 1994, Upchurch and Barrett 2000, Carballido and Pol 2010). In SHN (JJS) 140, 141 and 148, the mesial and distal wear facets slope lingually. Nevertheless, on these teeth, the apical wear facet faces labially, what could suggest a mandibular position. In conclusion, the wear pattern in morphotypes I and II begins with the appearance of a distal facet (e.g. SHN (JJS) 142, SHN 138), and then the mesial and apical facets appear (e.g. SHN (JJS) 140, SHN 508) and finally a 'V'-shaped facet develops. In morphotype III, the wear begins with a mesial facet (SHN 137), and then appear a distal and apical facets (SHN (JJS) 139) a finally a 'V'-shaped facet (SHN (JJS) 149). Additionally, in some teeth, it is possible to observe a wear facet on the medial/distal side of the base (e.g. SHN (JJS) 148, Figure 6(d)).

Discussion

Enamel-wrinkled texture, crown overlapping, spoon-shaped crowns and "V"-shaped wear facets were traditionally considered as synapomorphic traits of eusauropod teeth (Wilson and Sereno 1998). Nevertheless,

Figure 4. Heart-shaped teeth assigned to the morphotype II. SHN (JJS) 147 in apical (a.I), lingual (a.II), labial (a.III), distal (a.IV) and mesial (a.V) views; SHN 508 in apical (b.I), lingual (b.II), labial (b.III), distal (b.IV) and mesial (b.V) views; SHN 144 lingual (c.I), labial (c.II), distal (c.III) and mesial (c.IV) views; SHN 138 in apical (d.I), lingual (d.II), labial (d.III), distal (d.IV) and mesial (d.V) views; SHN 512 in apical (e.I), lingual (e.II), labial (e.III), mesial (e.IV) and distal (e.V) views; SHN 145 in apical (f.I), lingual (f.II), labial (f.III), distal (f.IV) and mesial (f.V) views; SHN 503 in apical (g.I), lingual (g.II), labial (g.III), distal (g.IV) and mesial (g.V) views; SHN (JJS) 141 in apical (h.I), lingual (h.II), labial (h.III), distal (h.IV) and mesial (h.V) views. Scale bar = 1 cm; grey circle = absent/weak worn; delimited grey circle = moderate worn; black circle = strongly worn.

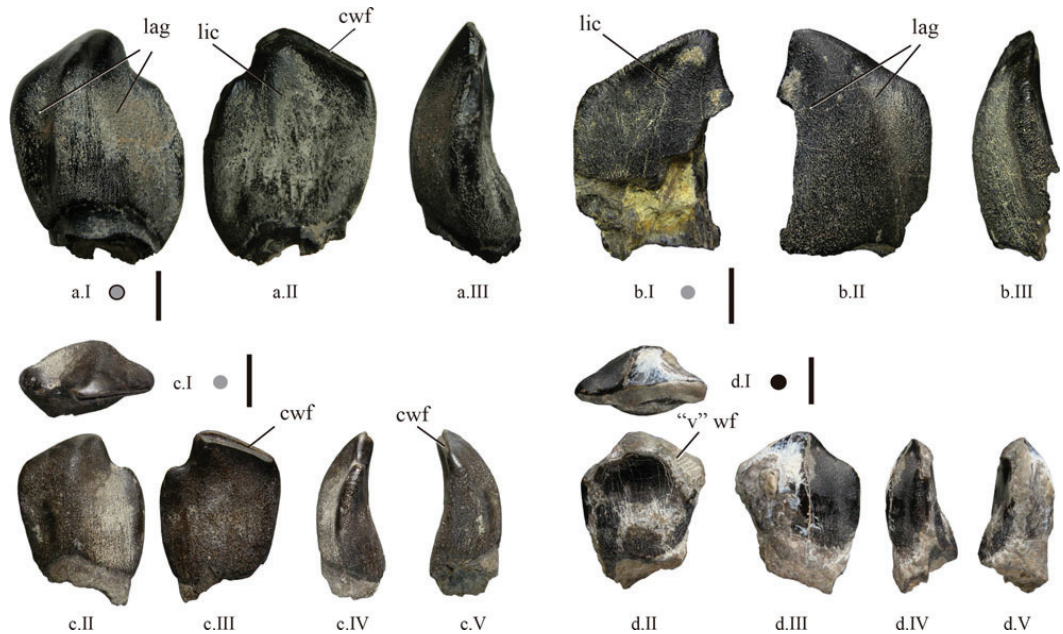

Figure 5. Heart-shaped teeth assigned to the morphotype III. SHN (JJS) 139 in labial (a.I), lingual (a.II) and distal (a.III) views; SHN (JJS) 146 in lingual (b.I), labial (b.II) and mesial (a.III) views; SHN 137 in apical (c.I), labial (c.II), lingual (c.III), distal (c.IV) and mesial (c.V) views; SHN (JJS) 149 in apical (d.I), lingual (d.II), labial (d.III), distal (d.IV) and mesial (d.V) views. Scale bar = 1 cm; grey circle = absent/weak worn; delimited grey circle = moderate worn; black circle = strongly worn.

recent works show that these features appear earlier than expected in sauropod evolution (e.g. Upchurch, Barrett, et al. 2007; Upchurch, Barrett, Xijin, et al. 2007; Yates 2007; Allain and Aquesbi 2008; Carballido and Pol 2010). Regardless of the morphological variability of the discussed teeth, we might tentatively relate these teeth to the Turiasauria clade based on the presence of the following diagnostic features proposed by Royo-Torres et al. (2006): (i) heart-shaped crowns; (ii) a pointed and asymmetrical apex that is strongly compressed labiolingually and (iii) crowns with convex labial surfaces with a bulge extending apicobasally. A pointed and asymmetrical apex that is strongly compressed labiolingually is well developed in *Turiasaurus* and the rest of the Iberian heart-shaped teeth. *Giraffatitan* also present a similar morphology for the apex (Janensch 1936). Crowns with convex labial surfaces with a bulge extending apicobasally are also shared with *Amygdalodon* (Carballido and Pol 2010), *Patagosaurus* (Bonaparte 1986) and *Tazoudasaurus* (Allain and Aquesbi 2008). Finally, besides the presence of several isolated heart-shaped teeth along the Middle Jurassic to Early Cretaceous, at the moment, the heart-shaped tooth morphology is exclusively related with the turiasaurs *Turiasaurus* (Royo-Torres et al. 2006; Royo-Torres and Upchurch 2012), *Zby* (Mateus et al. 2014) and a turiasaurian specimen with cranial and postcranial material from Villar del Arzobispo (Cobos et al. 2011). Heart-shaped morphology with pointed and asymmetrical apex that is strongly compressed labiolingually results in a so far exclusive combination of Turiasauria. The *Turiasaurus riodevensis* teeth (Royo-Torres et al. 2006; Royo-Torres and Upchurch 2012) are particularly similar to those of the morphotype II identified in the Portuguese Upper Jurassic, and some of them are virtually indistinguishable. The phylogenetic revision of the Iberian turiasaurs is in progress, which will include some new specimens, and will provide new information about the phylogenetic distribution of these characters along the eusauropod evolutionary history.

The SI values of our sample range between 1.1 and 1.8 and are probably related with the tooth morphology: lower, intermediate and higher SI values correspond to morphotypes III, II and I, respectively. This index was defined by Upchurch (1998) and it have been used to compare taxa and to understand evolutionary trends in teeth morphology and feeding mechanisms (e.g. Salgado and Calvo 1997; Barrett et al. 2002; Barrett and Wang 2007; Wilson and Upchurch 2009; Chure et al. 2010; Mannion 2010; Saegusa and Tomida 2011). Several eusauropods and basal macronarians with spoon- or

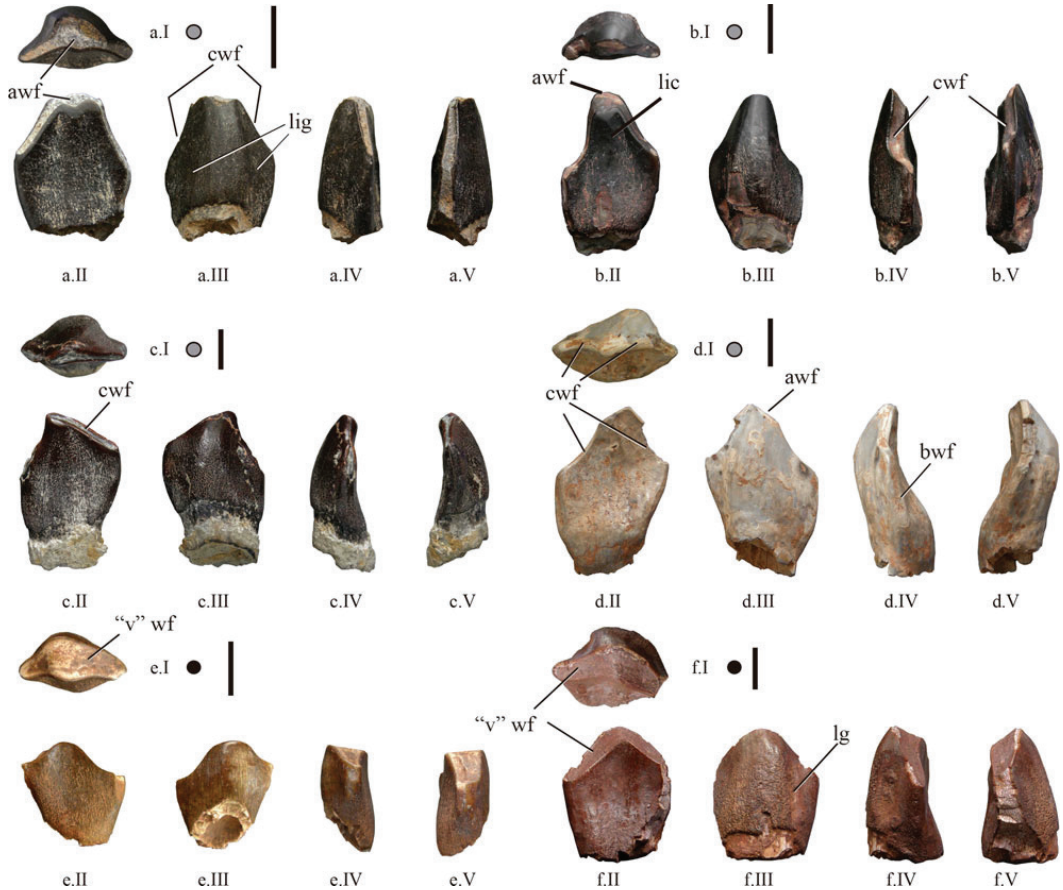

Figure 6. Heart-shaped teeth with marked worn. SHN (JJS) 131 in apical (a.I), lingual (a.II), labial (a.III), mesial (a.IV) and distal (a.V) views; SHN 152 in apical (b.I), lingual (b.II), labial (b.III), distal (b.IV) and mesial (b.V) views; SHN (JJS) 127 in apical (c.I), lingual (c.II), labial (c.III), distal (c.IV) and mesial (c.V) views; SHN (JJS) 148 in apical (d.I), lingual (d.II), labial (d.III), mesial (d.IV) and distal (d.V) views; SHN (JJS) 130 in apical (e.I), lingual (e.II), labial (e.III), mesial (e.IV) and distal (e.V) views; SHN (JJS) 129 in apical (f.I), lingual (f.II), labial (f.III), mesial (f.IV) and distal (f.V) views. Scale bar = 1 cm; grey circle = absent/weak worn; delimited grey circle = moderate worn; black circle = strongly worn.

spatulate-shaped teeth bear SI ranges with the same magnitude (see Supplementary material of Chure et al. 2010).

Modified from Chure et al. (2010), in Figure 7 we plotted the logged SI values found in the Portuguese Upper Jurassic heart-shaped teeth (excluding teeth with strong wear) together with other sauropodomorphs. The average for SI in *Turiasaurus* teeth (1.25) and in the Portuguese specimens (1.40) is slightly different, probably due to the size of the sample (three teeth) for *Turiasaurus*, which is composed by teeth with a morphology close to those of the morphotype II. Nevertheless, the SI average of *Turiasaurus* fits in the range of the Portuguese Upper Jurassic heart-shaped teeth. The SI range of our sample does not show any particular trend and they set within the morphospace occupied by non-neosauropod sauropods (Figure 7) as well as, *Turiasaurus* teeth. The presence of SI values close to 1 fits the morphotype III outside the morphospace occupied by the non-neosauropod sauropods.

We also plotted the Log_{10} SI for Sauropodomorpha, non-neosauropod eusauropods and five sauropod clades: Diplodocoidea, Brachiosauridae, Euhelopodidae and Lithostrotia (using Chure et al. 2010; D'Emic et al. 2013 data; see Appendix 2) versus the number of genera that have teeth included in our data (Figure 8). *Turiasaurus riodevensis* and the Portuguese Upper Jurassic heart-shaped are plotted together and they show a narrow range

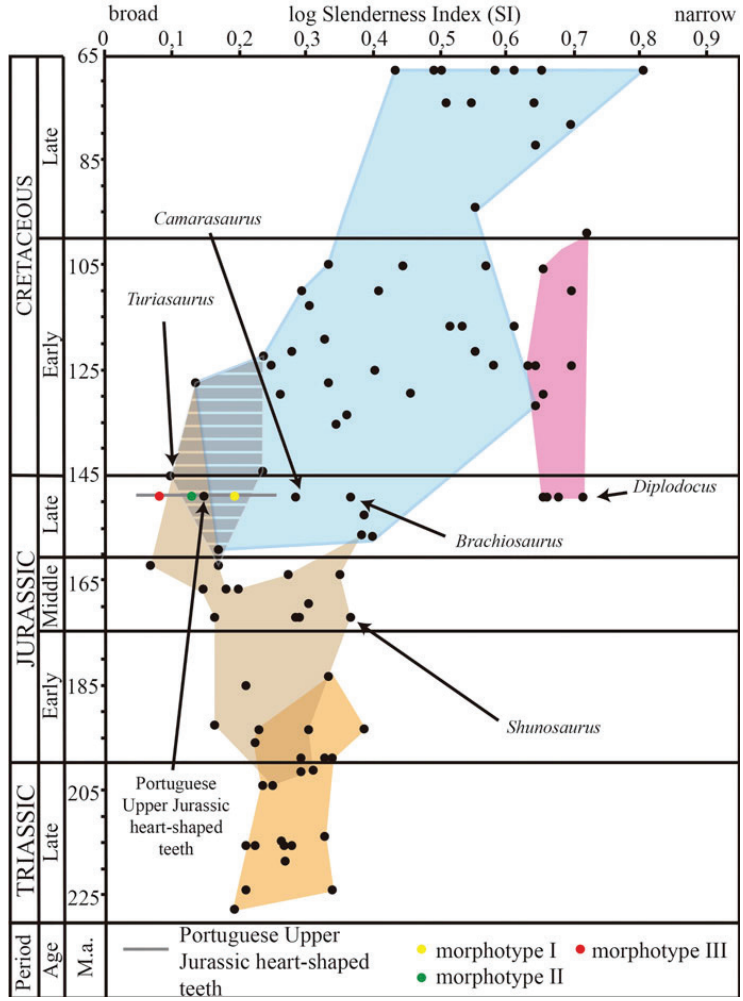

Figure 7. Temporal patterns in sauropodomorph tooth shape modified from Chure et al. (2010). The plot shows the logged tooth SI for sauropodomorph genera throughout the Mesozoic. Orange field indicates non-sauropod sauropodomorphs, brown field indicates basal sauropods, pink field indicates diplodocoids and blue field indicates macronarians. The uncertain phylogenetic position of *Jobaria* is indicated by cross-hatching; the transparent blue and brown fields indicate that the shape of the tooth space when *Jobaria* is included within macronarians and basal sauropods, respectively. Time scale based on Gradstein et al. (2004). The grey line is the SI range of the Portuguese Upper Jurassic teeth; the yellow, green and red circles represent the average Log (SI) for morphotypes I, II and III, respectively.

than diplocoids, brachiosaurids or mamenchisaurids (a narrow range of the former two groups was previously noted by D'Emic et al. 2013).

Ortega et al. (2010) have already related SHN (JSS) 139 (Figure 4(a)) and 140 (Figure 3(a)) to *Turiasaurus*. Royo-Torres et al. (2006, 2009) included in Turiasauria a tooth housed in the Museu Geológico (MG 4832, Figure 9 (a)) from the Alcobaça Formation in São Martinho do Porto (lower Kimmeridgian), as well as a tooth (MUJA-0635) found in the Upper Jurassic of Asturias (Spain) (Martínez et al. 2000). Mateus (2009) assigned as *Turiasaurus riodevensis* a tooth and postcranial material (ML 368) found in Vale das Pombas (Lourinhã), previously related with *Camarasaurus* (Mateus 2005), and now part of the *Zby atlanticus* holotype (Mateus et al. 2014). Two other sauropod teeth referred by Sauvage (1897–98) as '*Pelorosaurus humerocristatus*' (Hulke 1874) found in Fervença (MG 277, Figure 9(a)) (lower

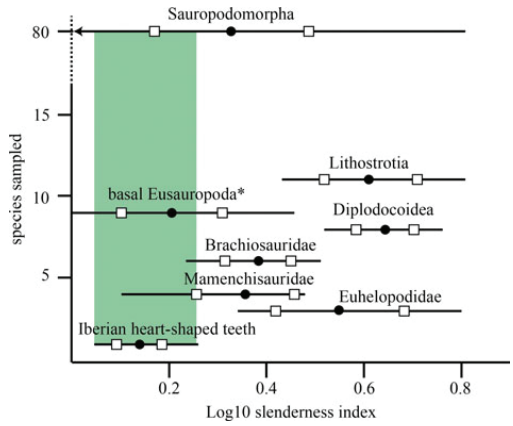

Figure 8. Crown Log_{10} (SI) versus the number of genera known from teeth in Sauropodomorpha and derived clades (modified from D'Emic et al. 2013). The mean (black circle), standard deviation (white square) and range (horizontal line) of tooth breadth for each clade are indicated (log_{10} Sauropodomorpha slenderness index range extends towards zero as indicated by the arrow). Green field shows the Log_{10} (SI) range Turiasauria compared to other sauropodomorph clades. *Not including neosauropods, mamenchisaurids, turiasaurs and putative eusauropods with uncertain phylogeny such as *Datousaurus*.

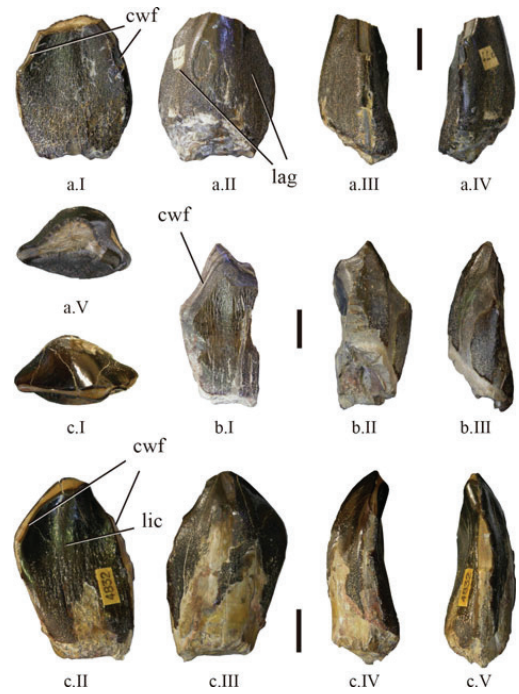

Figure 9. Heart-shaped teeth from Museu Geológico. MG 277 in lingual (a.I), labial (a.II), distal (a.III), mesial (a.IV) and apical (a.V) views; MG 16 in lingual (b.I), labial (b.II), mesial or distal (b.III) views; MG 4832 in apical (c.I), lingual (c.II), labial (c.III), mesial (c.IV) and distal (c.V) views. Scale bar = 1 cm.

Kimmeridgian, Alcobaça Fm.) and Ourém (middle-to-upper Oxfordian, Montejunto Fm. or Kimmeridgian-basal Tithonian, Alcobaça Fm.) (MG 16, Figure 9(b)), also bear a heart-shaped morphology.

Royo-Torres et al. (2006, 2009) also included in Turiasauria the heart-shaped teeth related to '*Neosodon*' (invalid taxon according to Upchurch et al. 2004) from the Tithonian of France (figured in Buffetaut and Martín 1993). Royo-Torres et al. (2009) distinguished them from *Turiasaurus* because they exhibit a more concave lingual face and a greater apicobasal development in the terminal part of apex, a feature shared with the herein proposed morphotype I. In fact, it is possible to identify, at least, two of the three morphotypes defined in this study, morphotypes I (BHN2R 113 and BHN2R 1102) and II (BHN2R 1101) (see figured teeth in Buffetaut and Martín 1993). Buffetaut and Martín (1993) also assigned to '*Neosodon*' the teeth found in Fervença and Ourém, referred earlier. The morphological features present in the heart-shaped teeth of the French Upper Jurassic are not diagnostic and they share their overall morphology with heart-shaped teeth of Iberian Upper Jurassic (e.g. Royo-Torres et al. 2006; Mateus et al. 2014; this work) or the Middle/Upper Jurassic of the UK (Figure 10(a)–(c),(e)); Royo-Torres and Upchurch 2012) and the Lower Cretaceous of France (Néraudeau et al. 2012) and the UK (e.g. Figure 10(d), Lydekker 1888, 1889; Upchurch et al. 2011). '*Neosodon*' must be considered an invalid taxon because of the absence of diagnostic features. The teeth should not be used as infrageneric determinations as noted, for example, Canudo et al. (2002) or García and Cerda (2010). The SI for '*Neosodon*' teeth (≈1.26–1.64) was obtained using the figured specimens on Buffetaut and Martín (1993), and fits in the SI range of Portuguese heart-shaped teeth.

Buffetaut and Martín (1993) also warn for the similarities among '*Neosodon*' teeth and the *Cardiodon* tooth from the British Bathonian. The specimen of *Cardiodon* figured in Owen (1844, 1875) shows a similar morphology to that found in *Turiasaurus* and '*Neosodon*', which allowed Royo-Torres et al. (2006, 2009) to consider it as a Turiasauria member. *Cardiodon* is included in Eusauropoda because it has teeth with a broad spatulate outline, wrinkled enamel and a groove on the labial surface near the distal margin (Upchurch et al. 2004). The name *Cardiodon* has been retained because some authors consider that there are is distinct character to all other known spoon-like sauropod teeth: mildly convex lingual face (Upchurch and Martin 2003; Upchurch et al. 2004; Mannion 2010). However, there are other sauropods with

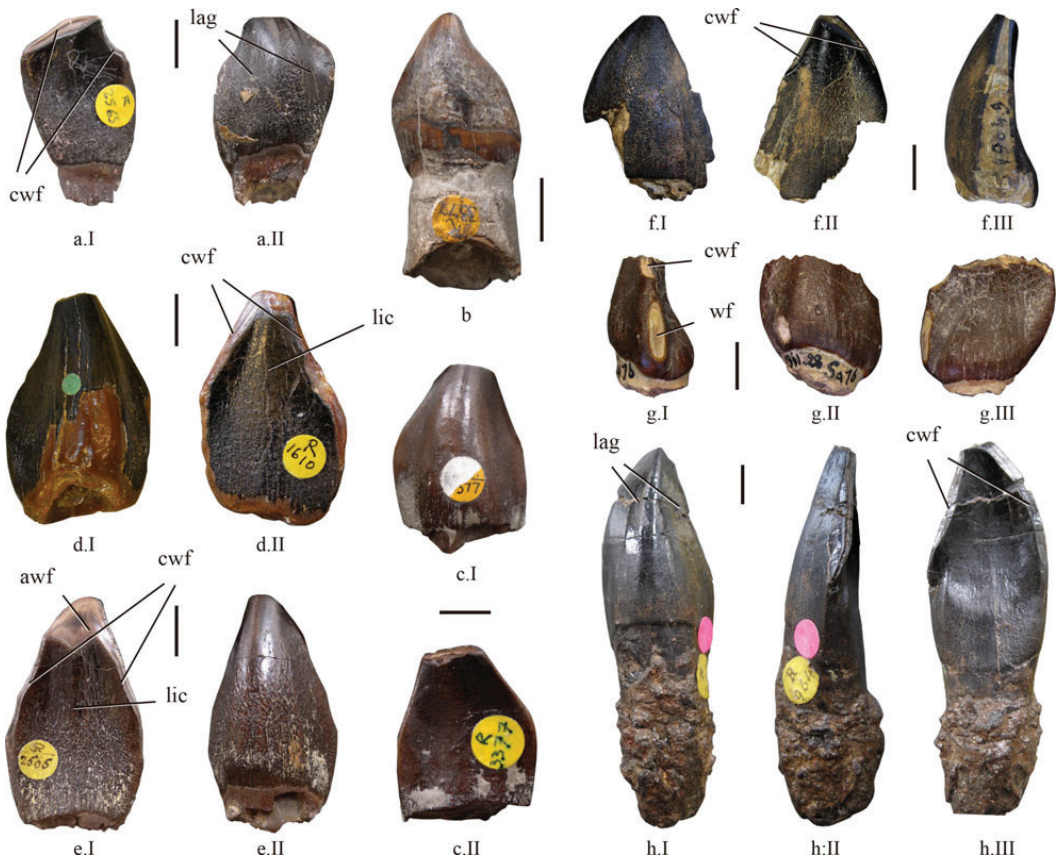

Figure 10. Heart-shaped teeth from Middle-Early Cretaceous outside Iberian Peninsula. NHMUK R2565 in lingual (a.I) and labial (a.II) views; NHMUK R3377 in lingual view (b); NHMUK R3377 in labial (c.I) and lingual (c.II) views; NHMUK R1610 in labial (d.I), lingual (d.II) views; NHMUK 2565 in lingual (c.I), labial (c.II) views; Middle Jurassic tooth of Madagascar (MNHN.F MAJ 423) in labial (f.I), lingual (f.II) and distal (f.III) views; Middle Jurassic (?) tooth of Niger (MNHN.F 1961-28) in distal (g.I), labial (g.II) and lingual (g.III) views. Holotype of *Oplosaurus* (Lower Cretaceous NHMUK R.964) in labial (h.I), distal (h.II) and lingual (h.III) views; Scale bar = 1 cm.

spoon-shaped teeth that also bear a convex lingual face, such as *Amygdalodon* (Carballido and Pol 2010). Furthermore, the heart-shaped teeth discussed here have a transversely convex lingual face at the base of the crown, which becomes transversely flat to slightly concave apically. This condition is also observed in a tooth referred to '*Cardiodon rugolosus*' (Steel 1970; Upchurch and Martin 2003; NHMUK R1527) which has a transversely convex lingual face at the base of the crown and transversely flat to slightly concave lingual face apically. Taking into account the absence of a detailed description and figuration of this tooth, which allows testing the exclusivity of *Cardiodon* tooth morphology, and the loss of this specimen, we regard *Cardiodon* as *nomina dubia*, till the discovery of the type specimen or related information. Three teeth from the Lower Oxford Clay (middle Callovian) of Cambridgeshire (Martill 1988; Barrett 2006) previously assigned to '*Cetiosauriscus leedsi*' (NHMUK R3377, Figure 10(b),(c)) also preserve a heart-shaped morphology previously related to Turiasauria (Royo-Torres and Upchurch 2012). Several specimens referred to '*Hoplosaurus*' and '*Pelorosaurus*' from the Upper Jurassic of the UK (NHMUK R2822, NHMUK R2565, NHMUK R2004-5, Figure 10(a),(e)) also fit in the general morphology here described.

Buffetaut and Martín (1993) pointed the similarities between '*Neosodon*' and *Camarasaurus* teeth. Furthermore, Mateus (2005) related preliminary the *Zby* holotype with a heart-shaped tooth to *Camarasaurus* genus. However, it is possible to identify some differences in

Camarasaurus teeth (e.g. Osborn and Mook 1921; Ostrom and McIntosh 1966; McIntosh et al. 1996): (i) generally higher than heart-shaped teeth (SI: 1.53–2.447 *sensu* Chure et al. 2010); (ii) distal and mesial edges are straight and almost parallel in the base of the crown, while just the morphotype I of the heart-shaped teeth shows some degree of straightness and parallelism; (iii) the former shows shorter apices; (iv) *Camarasaurus* bears lingual facets and a marked and complex cingulum on the lingual face; (v) a lingual crest that appears only in the apex sector; (vi) lack of heart-shaped morphology that probably characterises the Turiasauria clade (the heart-shaped morphology fits in the spoon-shaped morphology and *Camarasaurus* was characterised by a spatulate-shape morphology); (vii) lingual projection of apex more pronounced than heart-shaped teeth; (viii) the labial face of the apex is more inflated and globose in *Camarasaurus* teeth. The most distal teeth of *Camarasaurus* could share some of these features with heart-shaped teeth.

In Europe, the heart-shaped morphology is not exclusive from the Middle and Upper Jurassic, being identified a few occurrences in the Lower Cretaceous. From Hauterivian-Barremian sediments of Angeac, in France, were found heart-shaped teeth (Néraudeau et al. 2012). Néraudeau et al. (2012) noted the similarities between the morphology of these teeth with *Turiasaurus riodevensis* and other Jurassic and Cretaceous occurrences. In the UK and Spain, there are also some heart-shaped teeth occurrences: (i) the Lower Cretaceous tooth figured in Lydekker (1889, NHMUK R1610, Figure 10(d)) from Wealden Group dated to Barremian-lower Aptian (Naish and Martill 2001), (ii) the holotype of *Oplosaurus armatus* Gervais 1852 from the Lower Cretaceous of the Isle of Wight (Figure 10(h); NHMUK R964, Wessex Formation, Lydekker 1888; Upchurch et al. 2011), and (iii) two teeth (CPT-678 and PBA-2) from the Hauterivian-Barremian (El Castellar Formation) of El Castellar and Galve localities (Teruel) referred to *Oplosaurus armatus* (Royo-Torres and Cobos 2007). Nevertheless, *Oplosaurus*, El Castellar and Galve teeth show some morphological features not yet identified in Upper Jurassic heart-shaped teeth such as the presence of vertically and mesiodistally oriented apical wear facets and the presence of lingual facets and a complex cingulum morphology that is also found in *Camarasaurus* or *Euhelopus* (e.g. Ostrom and McIntosh 1966; Wilson and Upchurch 2009).

Three teeth from Africa are related to the heart-shaped morphology. From the Middle Jurassic sediments of Madagascar, more precisely in Ankinganivalaka site (Läng 2008), was found a tooth (MNHN.F MAJ 423, Figure 10(f)) with an almost complete crown. This crown bears the typical heart-shaped morphology present in the morphotype II defined here. Another tooth (MNHN.F 1961-28, Figure 10(g)) from In Gall (Niger) (Lapparent 1960) also bears a heart-shaped morphology shared by the morphotype II. This tooth came from Irhazer Group sediments, probably not younger than upper Middle Jurassic (Rauhut and López-Arbarello 2009). Finally, another tooth (UT-TEN15) from Tendamirah Quarry, Cabao Formation (Hauterivian-Barremian) in Libya (Le Loeuff et al. 2010) has a basal constriction and a crown similar to the morphotype I, and lacks the complex cingulum with associated lingual facets present in *Camarasaurus* or *Euhelopus* (Ostrom and McIntosh 1966; Wilson and Upchurch 2009).

Until the end of the twentieth century, neosauropod postcranial references dominate in Portuguese Upper Jurassic. This is incongruent with the relative abundance of these type teeth morphology assigned to Eusauropoda. However, the specimen of Vale das Pombas, *Zby atlanticus* (Mateus 2009; Mateus et al. 2014), and some new material in study, show that the occurrence of eusauropod postcranial material is not so rare. Therefore, the hypothesis that these teeth belong to a neosauropod form by convergence, or that this morphology corresponds to a more inclusive group than Turiasauria is not ruled out. New discoveries are necessary to confirm the link between these teeth and the occurrences related to Turiasauria.

Royo-Torres et al. (2006, 2009) and Royo-Torres and Upchurch (2012) considered that the heart-shaped morphology could be referred to the Turiasauria. At the moment, *Turiasaurus* and *Zby* are the only turiasaurs with cranial and postcranial materials. In the light of some recent phylogenetic approaches (Royo-Torres et al. 2006, 2009, 2012; Royo-Torres, Upchurch, et al. 2014; Royo-Torres, Cobos, et al. 2014; Royo-Torres and Upchurch 2012; Mocho, Royo-Torres, et al. 2014; Mocho, Royo-Torres, Malafaia, et al. 2014), the non-neosauropod eusauropods have spoon-shaped teeth. If *Turiasaurus*, *Losillasaurus*, *Galveosaurus* and *Zby* correspond to a monophyletic clade, their heart-shaped teeth could be considered as a synapomorphy of Turiasauria (the condition is unknown in *Galveosaurus* and *Losillasaurus*). However, the presence of this type of tooth morphology in the Middle Jurassic to the Lower Cretaceous of Africa and Europe put in evidence that this particular morphology has a wider stratigraphic and paleogeographic distribution, that could reflect a wider phylogenetic distribution.

Other possibility is to consider that this morphology was acquired by convergence in several sauropod groups. This hypothesis could explain the presence of this tooth morphology in the Middle Jurassic of the UK and in the Lower Cretaceous of France and the UK, where it was not yet found or documented other turiasaurian cranial (non-teeth material) and postcranial remains. The presence of convergences in sauropod tooth morphology has already been identified between diplodocids and titanosaurs (e.g. Salgado and Calvo 1997) or mamenchisaurids and some macronarians (e.g. Suteethorn et al. 2013). Convergence in tooth

morphotypes has also been suggested for brachiosaurids and titanosaurs (Chure et al. 2010) and both with euhelopodids (D'Emic et al. 2013).

The differences shown by the three proposed morphotypes can be explained by two different ways (or a combination of both): (i) the three morphotypes represents three distinct taxa (in generic or specific level) inside or outside the Turiasauria clade (this morphology could not be exclusive of the clade); or (ii) the three morphotypes belong to the same taxon and the variability is associated to a distinct position along the tooth row, as occurs in other sauropods such as *Giraffatitan* (Janensch 1936), *Camarasaurus* (Gilmore 1925), *Abydosaurus* (Chure et al. 2010) or *Euhelopus* (Wiman 1929; Wilson and Upchurch 2009; Poropat and Kear 2013). A slight heterodonty was also suggested for the skull of *Turiasaurus riodevensis* (Royo-Torres and Upchurch 2012). The distinct wear pattern observed along the morphotypes also could be explained in the same way, or might represent a distinct taxon or are function of the tooth row position.

Observing the variation in teeth morphology along the tooth row for *Camarasaurus* (Gilmore 1925) or *Giraffatitan* (Janensch 1936), some remarkable trends to the distal part of the tooth row can be enumerated: (i) decreasing of SI value (SI value varies at least a unit in both taxa: *Camarasaurus* ≈2.7–1.7; and *Giraffatitan* ≈3.5–2.5); (ii) decreasing of apex height; (iii) prominence in distal curvature of the apex; and (iv) progressive medial tooth imbrication. Assuming that the teeth described belong to a single taxon, the defined morphotypes (I, II and III) could represent different positions in tooth row fitting well in the variability observed for *Camarasaurus* (Gilmore 1925) or *Giraffatitan* (Janensch 1936). In this case, morphotype I should correspond to an anterior position, morphotype III to a more posterior position, and morphotype II located between morphotypes I and III. It is necessary to have a well-represented *in situ* tooth sequence of a turiasaurian individual to confirm if the three morphotypes fit in the range of a unique species or otherwise some of the morphotypes represent distinct taxa (inside or outside Turiasauria). Anyway, taking into account the variability present in other taxa, the variation in teeth morphology along the tooth row of a unique taxa seems to be the most parsimonious hypotheses to explain the morphological variability in the Iberian sample.

Conclusions

Forty-three heart-shaped teeth from the Portuguese Upper Jurassic were described and tentatively referred to Turiasauria based on the presence of a heart-shaped crown and a pointed and distally projected apex. Till today, this tooth morphology was the only one found associated with skeletal remains in *Turiasaurus* and *Zby*, both considered as members of Turiasauria, suggesting that the heart-shaped morphology could be referred as a possible synapomorphy of this clade. This sample shows a great variability among which can be recognised three different morphotypes: *morphotype I*, high SI (1.8–1.6) values and high apex (an half of tooth total height), *morphotype II*, moderate apex and SI values (1.5–1.3), with well defined heart-shaped and more strong distal deflection; *morphotype III*, low SI values (<1.3) and extremely low apex, with heart-shaped to subsquared-shaped form. Morphotypes I and II set within the morphospace occupied by other non-neosauropod sauropods, with the exception of the morphotype III, with lower SI values.

To explain the present morphological variability, two hypotheses (or combination of both) were mainly discussed: (i) these teeth belong to distinct taxa outside or inside Turiasauria or (ii) these teeth correspond to different positions on the tooth row of unique taxa. The morphological disparity shown by few sauropods (e.g. *Turiasaurus* or *Camarasaurus*) along tooth row suggests that this variability could be explained by a slightly heterodonty with morphotypes I, II and III located in mesial, middle and distal position, respectively. The presence of several teeth in different states of wear allows proposing a hypothetical general wear pattern for morphotypes I, II and III. In the former two morphotypes, the wear begins with the appearance of a distal facet, then the appearance of mesial and apical facets and finally a 'V'-shaped facet. In morphotype III, the wear seems to begin with the appearance of a mesial facet.

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CHAPTER 9

First occurrences of basal eusauropod procoelous caudal vertebrae in the Portuguese Upper Jurassic

First occurrences of basal eusauropod procoelous caudal vertebrae in the Portuguese Upper Jurassic

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9.1. INTRODUCTION

The Upper Jurassic Lusitanian Basin (Portugal) is known by the abundant occurrences in fossil vertebrates, in particular, dinosaurs, turtles and crocodyliforms (e.g. Sauvage, 1897-98; Lapparent and Zbyszewski, 1957; Dantas, 1990; Antunes and Mateus, 2003; Mateus, 2006; Ortega et al., 2006, 2008, 2013; Pérez-García and Ortega, 2011). The sauropod fossil record is particularly rich in this basin with several classical references (e.g. Sauvage, 1897-98; Lapparent and Zbyszewski, 1957). At present, the group is represented by four taxa: the camarasaurid *Lourinhasaurus alenquerensis* (Lapparent and Zbyszewski, 1957; Dantas et al., 1998; Mocho et al., 2014a); the diplodocid *Dinheirosaurus lourinhanensis* (Bonaparte and Mateus, 1999; Mannion et al., 2012), the basal macronaria *Lusotitan atalaiensis*, a putative brachiosaurid with doubt (Lappatent and Zbyszewski, 1957; Antunes and Mateus 2003; Mannion et al. 2013) and the turiasaur *Zby atlanticus* (Mateus et al., 2014).

Despite the recent systematic revision of the Portuguese Upper Jurassic taxa (*Dinheirosaurus* and *Lusotitan*, Mannion et al. 2012, 2013a; and *Lourinhasaurus*, Mocho et al. 2013a, 2014), several new occurrences (Royo-Torres et al., 2006, 2009; Yagüe et al., 2006; Mateus, 2009; Ortega et al., 2010; Mannion et al., 2012, Mocho et al., 2012, 2013b, 2014b; Mateus et al., 2014) have been recently referred, denoting a more diverse scenario for sauropods in the Lusitanian Basin during the Upper Jurassic. The basal eusauropod group Turiasauria (Royo-Torres et al., 2006) was recently identified in the Upper Jurassic sediments of this basin (Mateus, 2009; Royo-Torres et al., 2009; Ortega et al., 2010; Mocho et al., 2012, in press; Royo-Torres et al., 2012). Mateus et al. (2014) defined a new turiasaur genus and species, *Zby atlanticus*, collected from Vale de Pombas. This specimen was firstly related to *Camarasaurus* (Mateus, 2005) and posteriorly to *Turiasaurus riodevensis* (Mateus 2009). *Zby* was considered as a member of the Turiasauria clade (Mateus et al. 2014).

Herein, some procoelous caudal vertebrae found at the Upper Jurassic levels (Fig. 9.1a) in Baleal (Peniche), Paimogo, Praia de Areia Branca (Lourinhã) and Praia da Corva (Torres Vedras) are described and discussed. The presence of caudal vertebrae with convex posterior articular faces was acquired several times along the sauropod evolutionary history (e.g. Wilson and Sereno, 1998; Wilson, 2002; Upchurch et al., 2004; D'Emic, 2012; Mannion et al., 2013) such as in diplodocids, titanosaurs and mamenchisaurids (e.g. Salgado et al., 1997; Wilson and Sereno, 1998; Ouyang and Ye, 2002; Wilson, 2002; Gomani, 2005; Sekiya, 2011). In the Iberian realm, the procoelous condition is present in vertebrae of the Upper Jurassic Villar del Arzobispo Formation (Spain) assigned to members of Turiasauria (Casanovas et al., 2001; Royo-Torres et al., 2006, 2009), or to Diplodocidae (Royo-Torres et al., 2007). Nevertheless, so far, this type of vertebrae remained unknown in the Upper Jurassic of the Lusitanian Basin. The described procoelous caudal vertebrae were found in the sediments of the Praia de Amoreira-Porto Novo and Bombarral Formations (Fig. 9.1a-b) outcropping in the coastal region between Porto Novo and Baleal (e.g. Hill, 1988; Manuppella et al., 1999; Kullberg et al., 2006). These caudal vertebrae improves our knowledge on sauropods from the Portuguese Upper Jurassic, which include caudal vertebrae referred to brachiosaurids (Lapparent and Zbyszewski, 1957; Antunes and Mateus 2003; Mannion et al., 2013), camarasaurids (Yagüe et al., 2006; Mocho et al., 2013b, 2014a) and diplodocids (Mannion et al., 2012), allowing a better comparison with neighboring records.

9.2. ANATOMICAL ABBREVIATIONS

aca, anterior chevron articulation; cpol, centropostzygapophyses lamina; cr, caudal rib; pca, posterior chevron articulation; posl, postspinal lamina; prcdf, prezygapophyseal centrodiapophyseal fossa; prdl, prezygadiapophyseal lamina; prsl, prespinal lamina; spof, spinoprozygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprf, spinoprezygapophyseal fossa; sprl, spinoprezygapophyseal lamina.

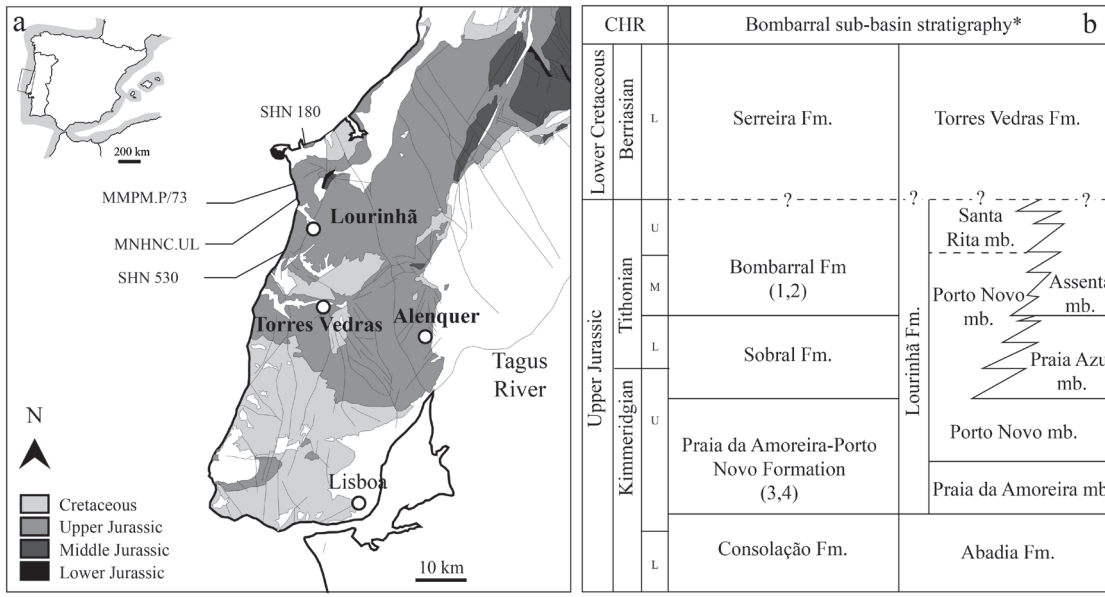

Figure 9.1. Geological map (adapted from Oliveira et al., 1992) showing the outcropping Portuguese Mesozoic levels and the localities of the described material found in Baleal (SHN 180), Paimogo (MMPM.P/73), Praia da Areia Branca (MNHN/UL.Din.027) and Praia da Corva (SHN 530). Stratigraphy proposed for the Bombarral Sub-basin by Manuppella et al. (1999) and Hill (1988, stratigraphy proposed for the coastal sector of Porto da Calada to Salir do Porto). Crn – Chronostratigraphy; *other formations are identified in Lourinhã region by Manuppella et al. 1999 as lateral correlatives of Bombarral Fm, 1 – Paimogo caudal vertebra (MMPM.P/73); 2 – Praia da Areia Branca caudal vertebra (MNHN/UL.Din.027); 3 – Baleal caudal vertebra (SHN 180); 4 – Praia da Corva caudal vertebra (SHN 530).

9.3. INSTITUTIONAL ABBREVIATIONS

HMN, Humboldt Museum für Naturkunde, Berlin, Germany; ML, Museu da Lourinhã, Lourinhã, Portugal; MG, Museu Geológico, Lisboa, Portugal; MMB.PALEO, Museu Municipal do Bombarral, Bombarral, Portugal (plus PALEO for the paleontological collection); MNHN/UL, Museu Nacional de História Natural e da Ciência, Universidade de Lisboa, Lisboa, Portugal; NHMUK, Natural History Museum, London, UK; SHN, Sociedade de História Natural, Torres Vedras, Portugal (plus (JJS) for the José Joaquim collection deposited in the Sociedade de História Natural)

9.4. SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842
Saurischia Seeley, 1887
Sauropodomorpha Huene, 1932
Sauropoda Marsh, 1878
Eusauropoda Upchurch, 1995
Eusauropoda indet.

9.4.1. Praia da Corva

Material: Incomplete anterior caudal vertebra (SHN 530). This vertebra is associated to several other remains including, sacral and caudal vertebrae, chevrons and appendicular elements.

Locality and horizon: Praia da Corva (Torres Vedras), Praia de Amoreira-Porto Novo Formation, upper Kimmeridgian-basal Tithonian in age (Manuppella et al., 1999).

Description: A centrum of a caudal vertebra is preserved including part of the caudal ribs (Fig. 9.2). This vertebra represents the most anterior caudal vertebra described herein considering the presence of a well-developed caudal rib. The centrum presents an oblique deformation. Without considering this deformation, the centrum probably would bear a subcircular-to-suboval outline, transversely compressed in anterior/posterior view. The centrum is slightly procoelous, i.e., the anterior articular face is concave, and the posterior one is slightly convex. The convexity of the posterior articulation is more pronounced than in MNHN/UL.Din.027, SHN 180 and MMPM.P/73 because this vertebra probably has a more anterior position in the tail. This convexity bears a central circular depression. In MNHN/UL.Din.027 and MMPM.P/73 are also found a small depression at the posterior articular face. The ventral face is convex, pierced by several small foramina, and transits continuously to the lateral face of the centrum without associated ventrolateral crests. The ventral border of the anterior articulation invades the ventral face of the centrum resulting in a flat platform probably for bridged chevrons. In the ventral border of the posterior articulation, this platform has a more rudimentary development. The lateral face lacks fossae or pleurocoels. Just below the left caudal rib, there is a small foramen.

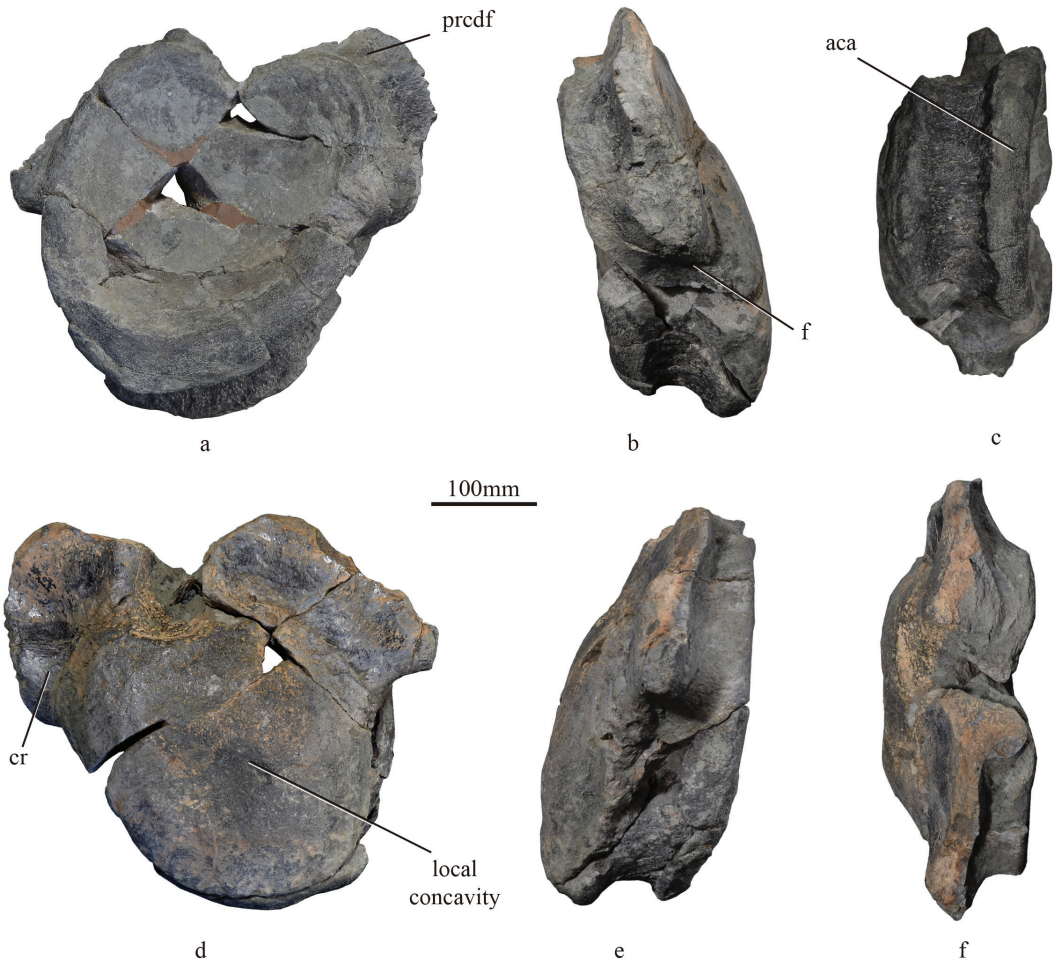

Figure 9.2. Anterior caudal vertebra of Praia da Corva (Torres Vedras, SHN 530) in anterior (A), left (B), ventral (C), posterior (D), right (E) and dorsal (F) views. Scale bar: 10cm

SHN 530 has the more developed caudal ribs of the studied sample. This caudal rib is laterally projected and bears a slight dorsal orientation (in anterior view) as occur in *Losillasaurus* (Lo-5, Casanovas et al., 2011). The ventral face of the caudal rib is slightly concave anteroposteriorly. Comparing with the anterior caudal ribs of other sauropods (Gallina and Otero, 2009), the SHN 530 caudal ribs are well developed and bear a fan-shaped morphology as occur in *Losillasaurus* (Casanovas et al., 2001) or *Mamenchisaurus* (Ouyang and Ye, 2002). Nevertheless, the dorsal development of SHN 530 caudal ribs is unknown. The caudal ribs are anteroposteriorly thinner. The left caudal rib presents a smooth concavity in the anterior and the posterior side at the same level. In the right caudal rib, this concavity is rudimentary. The posterior borders of the neural arch bear a ridge-like structure, suggesting the presence of a thick centropostzygapophyses lamina (cpol).

9.4.2. Praia da Areia Branca

Material: Anterior caudal vertebra (MNHN/UL.Din.027).

Locality and horizon: Praia da Areia Branca (Lourinhã), Bombarral Formation, Tithonian in age (Manuppella et al., 1999).

Description: This specimen correspond to an almost complete centrum of anterior caudal vertebra housed in the collections of the Museu Nacional de História Natural e da Ciência in Lisboa (Fig. 9.3). This vertebra is relatively large (see S.9) and bears a solid bone tissue. This specimen presents a procoelous centrum, i.e. a slight convex posterior articular face and a concave anterior one. On the convex posterior surface, there are a sinform-shaped pit. The centrum is subcircular in anterior/posterior views. Lateral margins are convex and slope medially. There are no fossae or pleurocoels on the lateral faces of this centrum. The ventral face is flat-to-convex and transversely short without associated ventrolateral crests. In the ventral margin of the anterior articular face, the articular facets for the chevrons correspond to a transversely elongated and flat platform, suggesting that the chevrons might be dorsally bridged. The ventral margin of the posterior articular face expands to the ventral face of the centrum also resulting in a transverse platform, not so well developed than the anterior one. The caudal ribs are dorsoventrally deep and seems to extends to the lateral face of the neural arch (not preserved). The dorsal margin of the caudal rib is generally rough and in its anterior margin there is a crest that could correspond to an incipient "prezygadipophyseal lamina" ("prdl"). This crest is generally well developed in the most anterior caudal vertebrae of *Giraffatitan* or *Abydosaurus* (Janensch, 1950; Chure et al., 2010). The caudal rib is laterally projected and transversely oriented.

9.4.3. Paimogo

Material: Anterior caudal vertebra (MMPM.P/73).

Locality and horizon: Paimogo (Lourinhã), Bombarral Formation, Tithonian in age (Manuppella et al. 1999).

Description: An incomplete anterior caudal vertebra (Fig. 9.4) housed in the paleontological collections of Museu Municipal de Porto de Mós is not fully prepared and lacks a big part of the neural arch and the distal end of the caudal ribs. The centrum is very similar to SHN 180 (described below), and they probably share a similar position, i.e. between 4th-8th caudal vertebrae. As SHN 180, the centrum is subcircular and slightly procoelous. The slightly convex posterior articular face bears a smooth concavity in the center of its dorsal half. The lateral faces of the centrum lack fossae or pleurocoels. The ventral face is convex-to-flat, without lateroventral crests, and not so transversely short than in SHN 180. Caudal ribs are dorsoventrally deep and progress to the lateral face of the neural arch. Caudal ribs are mainly laterally projected. In the anterior sector of the dorsal surface of the caudal ribs, there are some transversely oriented rugosities similar to those observed in the previous described vertebrae that might correspond to an incipient "prdl".

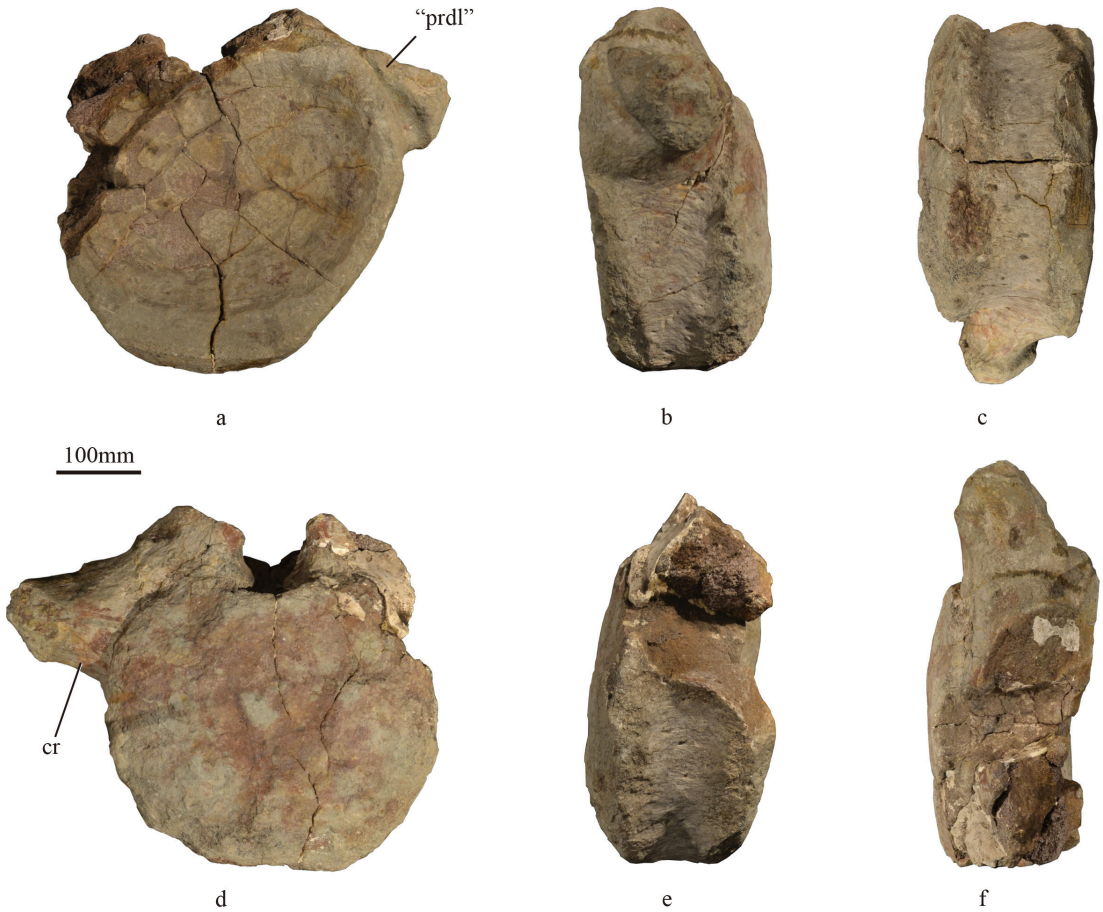

Figure 9.3. Anterior caudal vertebra of Praia da Areia Branca (Lourinhã, MNHN/UL.Din.027) in anterior (A), left (B), ventral (C), posterior (D), right (E) and dorsal (F) views. Scale bar: 10cm

9.4.4. Baleal

Material: A complete anterior caudal vertebra (SHN 180).

Locality and horizon: Baleal (Peniche municipality), Praia de Amoreira-Porto Novo Formation dated to upper Kimmeridgian-lower Tithonian (Manuppella et al., 1999).

Description: A proximal vertebra was recovered from the cliffs of Baleal (Peniche) (Fig. 9.5). Taking into account the presence of a deep caudal rib progressing to the lateral surface of the neural arch, and comparing with other well-known caudal series (e.g. Osborn and Mook, 1921; Bonaparte et al., 2000), this caudal vertebra probably corresponds to an anterior one, between 4th-8th caudal vertebrae. SHN 180 occupies a more posterior position than SHN 530, MNHN/UL.Din.027 and MMPM.P/73, and probably more posterior than the most posterior caudal vertebra figured for *Losillasaurus* (Lo-12; Casanovas et al., 2001). This is inferred by the presence of more developed caudal ribs and procoelous condition in SHN 530, MNHN/UL.Din.027 and MMPM.P/73. The centrum is slightly procoelous, i.e. with a concave anterior articular face and a slightly convex posterior one. The posterior articular face has marked convex borders and a central and small concavity. The centrum is subcircular in anterior and posterior views, and the articular faces bear

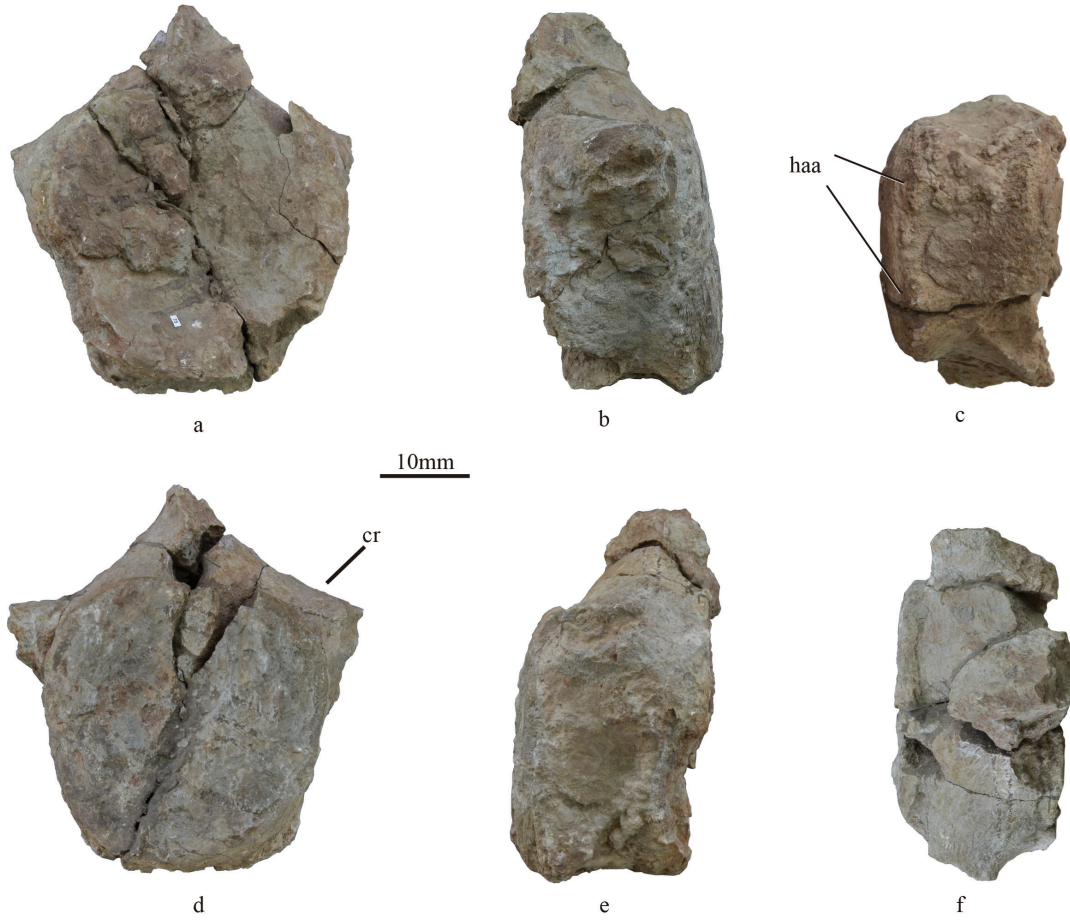

Figure 9.4. Anterior caudal vertebra of Paimogo (Lourinhã, MMPM.P/73) in anterior (A), left (B), ventral (C), posterior (D), right (E) and dorsal (F) views. Scale bar: 10cm

straight dorsal edges. The ventral surface is transversely compressed and convex. The anterior facets for the chevron have a semicircular outline, and the posterior ones extends slightly to the ventral surface of the centrum. The left caudal rib is lateroposteriorly projected, not reaching the level of the posterior articular face. The dorsal surface of the caudal ribs is deep, extending to the lateral surface of the neural arch. The anterior margin of the caudal rib is marked by a rough crest that are in the same position that the lamina that links the caudal rib to the point near or on the prezygapophyses (called by some authors as a "prdl", see Wilson et al., 2011). This lamina is also present in MNHN/UL.Din.027 and MMPM.P/73. The neural arch occupies almost all the dorsal surface of the centrum, being anteriorly displaced and slopping caudally. The neural arch lacks a profused lamination as occur in diplodocids (e.g. Hatcher, 1901; Lull, 1919; McIntosh, 2005; Remes, 2006). The neural spine slopes cranially and the dorsal margin of the spine slopes caudally in lateral view. The posterodorsal margin of the spine surpasses posteriorly the posterior articular face of the centrum. The neural spine is generally transversely compressed with a slight transverse expansion on its distal end. The neural spine is complete (only minor apical erosion) and is short (2/3 of the height of the centrum). The lateral face of the top of the neural spine bears a rough platform. The zygapophyses are particular large, as occur in *Losillasaurus* (Casanovas et al., 2001), being the maximum diameter larger than the

maximum transverse width of the neural spine. The articular facets of the prezygapophyses and postzygapophyses are subcircular and slopes medially (70º from the horizontal plane). The postzygapophyses have concave surfaces as occurs in some diplodocids (Whitlock, 2011). From the prezygapophyses and postzygapophyses part the spinoprezygapophyseal lamina (sprl) and the spinopostzygapophyseal lamina (spol), being the former specially marked. The spol becomes smoother in the basal quarter of the spine, only marked by a smooth ridge on the lateral face of the spine and bordering the postspinal lamina (posl). The sprl becomes pronounced up to the top of the neural spine. At the base of the spinoprezygapophyseal fossa (sprf), appears a rough prespinal lamina (prsl), which becomes wider up to the top of the neural spine (consequently the sprf disappears with the development of the prsl).

Figure 9.5. Anterior caudal vertebra of Baleal (Peniche, SHN 180) in anterior (A), left (B), ventral (C), posterior (D), right (E) and dorsal (F) views. Scale bar: 10cm

9.5. DISCUSSION

The caudal vertebrae described herein are featured by the presence of slightly convex posterior articular faces (incipient procoelous condition). All described procoelous vertebrae also present a restrict concavity on the convex posterior face. The presence of procoelous caudal vertebrae was considered diagnostic for some sauropod groups (e.g. Mamenchisauridae or Lithostrotia), being acquired several times along the sauropod evolutionary history (e.g. Wilson, 2002; Royo-Torres, 2009; Mannion et al., 2013). Nevertheless, SHN 530, SHN 180, MNHN/UL.Din.027 and MMPM.P/73 are differentiated in several ways from the morphology of the anterior caudal vertebrae of Titanosauria and Diplodocidae, and they are also different to those of mamenchisaurids.

The studied vertebrae are markedly distinct from the anterior caudal morphotype present in diplodocids such as in *Diplodocus* (Hatcher, 1901), *Barosaurus* (McIntosh, 2005) or *Tornieria* (Remes, 2006) or in a diplodocid specimen from Valmitão (SHN (JJS) 177; Mocho et al., 2014b). Because SHN 530, 180, MNHN/UL.Din.027 and MMPM.P/73 lack: *i*) deep pleurocoels (or fossae) in the lateral face of the centrum, *ii*) a strong concave ventral surface (ventral hollow) bordered by pronounced lateroventral crests, *iii*) "wing"-shaped caudal ribs, *iv*) rectangular neural spines in anterior/posterior view; *v*) spinoprezygapophyseal and spinopostzygapophyseal laminae contact; and *vi*) diapophyseal laminae present on caudal ribs (Wilson, 2002; Upchurch et al., 2004; Whitlock, 2011). The diplodocids generally present a slightly procoelous condition (e.g. Upchurch et al., 2004). This condition is more evident in the most anterior caudal centra in *Diplodocus* (Osborn, 1899; Hatcher, 1901; Lucas et al., 2006), *Barosaurus* (Lull, 1919; McIntosh, 2005) or *Apatosaurus* (Gilmore, 1936), and is more extensive along the tail in *Diplodocus* (Osborn, 1899; Hatcher, 1901; McIntosh, 2005). The turiasaurs also present a slight procoelous vertebrae such as in *Losillasaurus* (Fig. 9.6g-l, Casanovas et al., 2001) and in an anterior caudal vertebra (RD-13) from Puntal de Santa Cruz (Teruel, Spain; Villar del Arzobispo Fm.,Tithonian-lower Berriasian) referred to *Turiasaurus riodevensis* (Fig. 9.6d-f, Royo-Torres et al., 2009). SHN 530 and MNHN/UL.Din.027 were located in the most proximal sector of the tail, as occurs with the figured caudal vertebra of *Losillasaurus* (Lo-5; Casanovas et al., 2001). On the other hand, MMPM.P/73, SHN 180 and RD-13 occupy a more posterior position than SHN 530, MNHN/UL.Din.027, similar to Lo-12 in *Losillasaurus*.

SHN 530 presents the most developed caudal rib and procoelous condition. The caudal rib is not complete, but the preserved sector is very similar to the fan-like caudal rib present in *Losillasaurus* (Casanovas et al., 2001). Similar fan-like caudal ribs are also found in *Mamenchisaurus* (Ouyang and Ye, 2002), *Shunosaurus* (Zhang, 1988), *Omeiasaurus* (He et al., 1988) or *Haplocanthosaurus* (Hatcher, 1903). All these taxa share with the Praia da Corva specimen the laminar aspect of the caudal rib and the presence of a smooth concavity on its anterior side. This concavity is interpreted as a probable prezygapophyseal centrodiapophyseal fossa (prcdf, following Wilson et al., 2011). This fossa is not so deep and markedly bordered, particularly by the dorsal margin of the caudal rib, as in neosauropods such as *Camarasaurus* (e.g. Osborn and Mook, 1921; McIntosh et al., 1996), diplodocids (Osborn, 1899; Hatcher, 1901; Lull, 1919; Gilmore, 1936; Remes, 2006), rebbachisaurids (e.g. Torcida Fernández-Baldor et al., 2011; Mannion and Barrett, 2013) and some titanosauriforms (e.g. Janensch, 1950; Kellner et al., 2005). The prcdf are rudimentary or absent in dicraeosaurids (with well-developed caudal ribs; e.g. Janensch, 1929) and some titanosauriforms (Martínez et al., 2004; Calvo et al., 2007; Navarrete et al., 2011; D'Emic et al., 2013). The MNHN/UL.Din.027 and MMPM.P/73 share with *Losillasaurus* (Lo-12) a slight procoelous condition and the presence of laterally directed transverse process as well as ridge-like a rough "prdl", and they can not be distinguished.

The specimen HMN MB.R.2091.1-30 is a series of caudal vertebrae referred to "*Gigantosaurus*" *robustus* (now *Janenschia robustus*) by Janensch (1929) from the Upper Jurassic Tendaguru Formation (Upper Jurassic), also presenting strong-to-slight procoelous caudal vertebrae (Bonaparte et al., 2000). Higher neural spines and anterolateral directed caudal ribs differentiate

HMN MB.R.2091.1-30 from Portuguese specimens. HMN MB.R.2091.1-30 also presents a pronounced convex posterior articulation (Fig. 9.6m-r) in the most proximal centra as in some mamenchisaurids (Ouyang and Ye, 2002; Sekiya, 2011). Some authors suggested HMN MB.R. 2091.1-30 as a putative mamenchisaurid (Mannion et al., 2013a, b) by the presence of anterolateral projected caudal ribs and procoelous centra. Mamenchisaurids are featured by the presence of strong procoelous vertebrae (Upchurch et al., 2004) as in *Mamenchisaurus* (2002), *Omeisaurus* (Tang et al., 2001) and *Chuanjiesaurus* (Sekiya, 2011), becoming strongly pronounced in more proximal caudal vertebrae. Nevertheless, some specimens only show slight procoelous proximal caudal vertebrae (e.g. *Omeisaurus tianfuensis*, He et al., 1988). On the other hand, Royo-Torres and Cobos (2009) and Royo-Torres et al. (2014b) suggested that HMN MB.R.2091.1-30 is a putative African member of Turiasauria by the presence of an anterolateral projected caudal rib (not completely preserved) and procoelous centra (Royo-Torres et al., 2009). Four proximal (NHMUK R1984) caudal vertebrae belonging to a specimen referred to "*Cetiosaurus leedsi*" (Woodward, 1905) and the anteriormost caudal vertebrae of the *Cetiosauriscus* holotype (NHMUK R3087, Huene, 1927; Charig, 1993) from Middle Jurassic of United Kingdom, also present a slight procoelous condition (in "*Cetiosaurus leedsi*" with a central concave region as in the Portuguese Upper Jurassic specimens). These specimens have high neural spines, unlike SHN 180 but similar to *Losillasaurus* and HMN MB.R.2091.1-30. "*Cetiosaurus leedsi*" also shows a significant curvature of the neural spine, as in HMN MB.R.2091.1-30 and *Losillasaurus* (Bonaparte et al., 2000; Casanovas et al., 2001). SHN 180 and RD-13 present clear differences in the neural arch and caudal rib morphology respect to the anterior caudal vertebrae of *Losillasaurus*, HMN MB.R.2091.1-30, "*Cetiosaurus leedsi*" and *Cetiosauriscus stwerti*. However, these differences might be related with difference positions in the caudal series, corresponding the former to a rearmost position. The neural arch is not preserved in the Paimogo, Praia da Areia Branca and Praia da Corva specimens, so it is impossible to make a comparison with the rest of the specimens referred.

Some authors consider the presence of procoelous caudal centra as a synapomoporphy of Titanosauria (e.g. Wilson, 2002) that share the described specimens. Nevertheless, Carballido and Sander (2014) considered that titanosaurs bears a more pronounced procoelous condition on the anterior caudal vertebrae, also observed in some mamenchisaurids, that differs of the slight procoelous condition of diplodocids and some basal eusauropods non-mamenchisaurids such as *Losillasaurus* (Casanovas et al., 2011) or *Cetiosauriscus* (Huene, 1927; pers observ., PM). The caudal vertebrae reported herein might be distinguished from those groups of sauropods if we accept the marked procoelous condition as diagnostic for titanosaurs and for mamenchisaurids. In titanosaurs the posterior articulation are also marked by the presence of constricted condyles, as occurs in *Saltasaurus* (Powell, 1992) or *Lirainosaurus* (Díaz-Díez et al., 2012) and absent in the Portuguese specimens, *Losillasaurus* (Casanovas et al., 2001), the anterior caudal vertebra from Puntal de Santa Cruz (Royo-Torres et al., 2009) and HMN MB.R.2901.1-30 (Bonaparte et al., 2000). The presence of a ventral longitudinal hollow on the anterior and middle caudal vertebrae, considered as a synapomorphy of Titanosauria (Wilson, 2002; Upchurch et al., 2004; D'Emic, 2012), is also absent in SHN 530, 180, MNHN/UL.Din.027 and MMPM.P/73.

SHN 180 has a slight posterior projection of the caudal rib (left caudal rib almost laterally projected: Fig. 9.5). The pronounced posterior orientation of the caudal rib is considered as a synapomorphy of Titanosauriformes (Mannion and Calvo, 2011; D'Emic, 2012) and is present in the Upper Jurassic titanosauriforms *Giraffatitan* (Janensch, 1950) and *Lusotitan* (Mannion et al., 2013a), and *Galveosaurus* (Barco, 2009). The posterior orientation is not exclusive of the titanosauriforms and it is also present in some eusauropds such as *Spinophorosaurus* (pers. observ., PM), an undescribed turiasaur from the Villar del Arzobispo (RD-13, Cobos et al., 2011), *Cetiosaurus oxionensis* (Upchurch and Martin, 2003) and several sauropod specimens from the Middle Jurassic of Madagascar and Morrocco housed in Muséum national d'Histoire naturelle (e.g. Lapparent, 1955; pers. observ., PM).

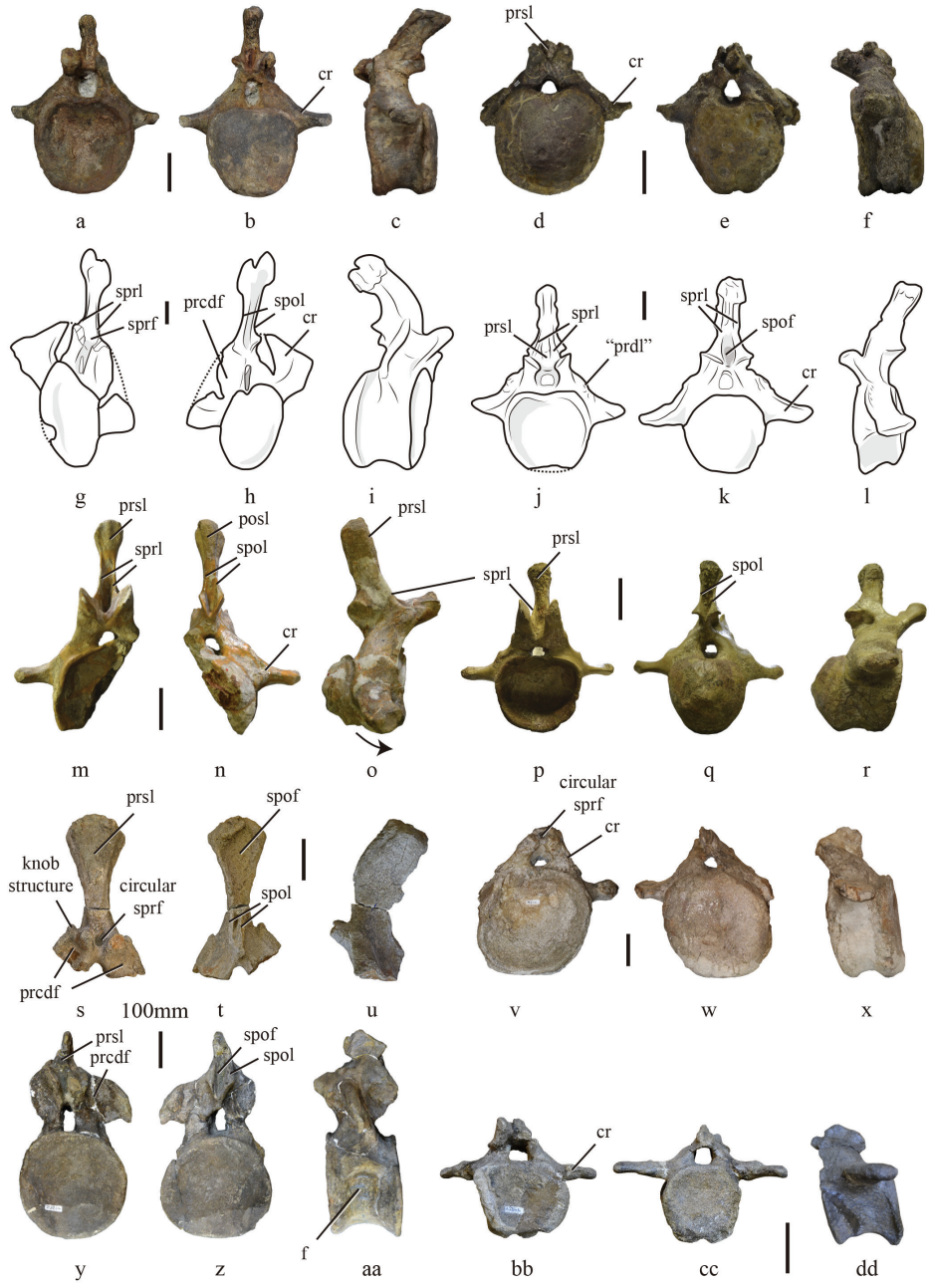

Figure 9.6. Anterior caudal vertebrae. SHN 180 in anterior (a), posterior (b) and left (c) views; Puntal de Santa Cruz anterior caudal vertebra referred to *Turiasaurus riodevensis* by Royo-Torres et al. (2009) in anterior (d), posterior (e) and left (f) views; Schematic draws based on Casanovas et al. (2001) of *Losillasaurus* anterior caudal vertebrae, Lo-5 in anterior (g), posterior (h) and right (i) views and Lo-12 in anterior (j), posterior (k) and left (l) views; HMN MB.R.2091.29 in anterior (m), posterior (n) and right (o) views; HMN MB.R.2094 in anterior (p), posterior (q) and right (r) views; *Lourinhasaurus alenquerensis* anterior caudal vertebrae, anterior neural spine (MG 30374) in anterior (s), posterior (t) and left (u) views, and anterior caudal centrum (MG 4956) in anterior (v), posterior (w) and left (x); *Lusotitan atalaiensis* anterior caudal vertebrae, MG 4985-2 and MG 4985-4 in anterior (y, bb), posterior (z, cc) and left (aa, dd) views, respectively. Scale bar: 10cm

Other feature considered as a synapomorphy of Titanosauriformes is the presence of a bulge or 'kink' on ventral margin of transverse process (D'Emic, 2012). The presence of a ventral bulge also appears in eusauropods such as *Losillasaurus*, RD-13 or *Spinophorosaurus* (Remes et al., 2009; pers. observ., PM) but is not developed in the described specimens of the Portuguese Upper Jurassic. The presence of a kink in a ventral crest-like structure coming from the distal end of the caudal rib is exclusive of some titanosauriforms such as *Giraffatitan* (Riggs, 1903, plate 2, fig. 1a), *Venenosaurus* (Tidwell et al., 2001, fig. 11.3) and *Tastavinsaurus* (Royo-Torres et al. 2009. fig. 5.51), and is absent in SHN 530, MNHN/UL.Din.027, MMPM.P/73 and also in *Losillasaurus* (Casanovas et al., 2001) and HMN MB.R.2901.1-30 (Bonaparte et al., 2000). This feature is generally present in more proximal vertebrae, being impossible to test accurately in the Baleal (SHN 180) and Puntal de Santa Cruz sauropod.

The caudal neural spine morphology in SHN 180 is relatively common in the anterior caudal vertebrae (excluding the most proximal vertebrae) of basal eusauropods and basal macronarians, with a stout sprl and spol that become softer in the basal quarter-half of the neural spine (with a slight displacement to the lateral face of the neural spine), transversely compressed neural spine, and dorsoventral short spof and sprf. SHN 180 bears a relative short neural spine considering it is an anterior caudal vertebrae, resembling the condition present in *Giraffatitan* (Janensch, 1950) but probably present in similar position in the RD-13 specimen, preliminary related with Turiasauria (Cobos et al., 2011).

In conclusion, SHN 180, 530, MNHN/UL.Din.027 and MMPM.P/73 share slight procoelous centra with the anterior caudal vertebrae of diplodocids and some basal eusauropods such as *Losillasaurus* or "*Cetiosaurus leedsi*". This condition is not considered the same as represented by the strong convex posterior articulations of titanosaurs, mamenchisaurids and the most proximal caudal of HMN MB.R.2901.1-30. The described vertebrae do not share the synapomorphic morphology (ventral hollow bordered by marked ventrolateral crests and the presence of pleurocoels or fossae in the lateral face of the centrum), which feature the anterior caudal vertebrae of diplodocids, a group recorded in the Upper Jurassic of the Iberian Peninsula (Bonaparte and Mateus, 1999; Royo-Torres et al., 2007, 2009; Mannion et al., 2012; Mocho et al., 2014b). Considering this, the available information suggest to consider SHN 180, 530, MNHN/UL.Din.027 and MMPM.P/73 as part of indeterminate eusauropod with slight procoelous condition, which probably corresponds to a non-mamenchisaurid basal eusauropod. The assignation of these procoelous anterior caudal vertebrae to a basal eusauropod form is congruent with the presence of eusauropods with procoelous anterior caudal vertebrae in the Iberian Upper Jurassic such as the turiasaur *Losillasaurus giganteus* (Casanovas et al., 2001). Several other specimens from the Upper Jurassic of the Iberian Peninsula are also related to Turiasauria including *Zby atlanticus* and *Turiasaurus riodevensis* (Royo-Torres et al., 2006, 2009; Mateus, 2009; Ortega et al., 2010; Mocho et al., 2012; Royo-Torres and Upchurch, 2012) suggesting that the described specimens might be related to this clade. *Losillasaurus giganteus* and *Turiasaurus riodevensis* (if is confirmed that the Puntal de Santa Cruz specimen belongs to this species) are the only Iberian Upper Jurassic taxa with this type of anterior caudal vertebra morphology. Nevertheless, the lack of information about other evolutionary novelties shared with turiasaurs prevent to confirm this possible relationship.

The presence of a short neural spines could be a convergence with the brachiosaurid *Giraffatitan*. This condition is absent in other brachiosaurids such as *Venenosaurus* (Tidwell et al., 2002), *Brachiosaurus* (Riggs, 1903) and *Cedarosaurus* (Tidwell et al., 1999), and is unknown in *Lusotitan* (Lapparent and Zbyszewski, 1957; Mannion et al., 2013a). A posterior position in the caudal series for the SHN 180 could explain this relative short neural spines when compared with other synchronic eusauropods. Furthermore, the absence of procoelous anterior caudal vertebrae in Brachiosuridae excludes, so far, the assignment of the specimen to that group.

9.6. PROCOELOUS VERTEBRAE IN THE CONTEXT OF THE IBERIAN SAUROPOD

Several caudal vertebrae, including partial caudal series, were recovered from the Upper Jurassic sediments of the Lusitanian Basin (e.g. Lapparent and Zbyszewski, 1957; Antunes and Mateus, 2003; Yagüe et al., 2006; Mateus, 2005), highlighting the caudal series of *Lusotitan atalaiensis* (Lapparent and Zbyszewski, 1957; Mannion et al., 2013a), the São Bernardino caudal series (MG 4978, Lapparent and Zbyszewski, 1957) and the probably indetermine Porto das Barcas sauropod (Sobral Fm., Lourinhã), previously referred to *Lourinhasaurus* (Antunes and Mateus, 2003; Mateus, 2005).

References to procoelous caudal vertebrae in the Iberian Upper Jurassic are scarce. Casanovas et al. (2001) quoted for the first time the presence of procoelous vertebrae in the description of *Losillasaurus giganteus*. The posterior articular faces in *Losillasaurus* vertebrae are moderately convex to slight convex along the tail (Casanovas et al., 2011). This condition is present in all recovered caudal vertebrae, and so, at least, up to the 6th caudal vertebra (Fig. 9.7). Royo-Torres et al. (2009) also referred a slight procoelous vertebra from the Puntal de Santa Cruz, that they assign to *Turiasaurus riodevensis*. *Turiasaurus* and *Losillasaurus* belong to a monophyletic clade, Turiasauria (Royo-Torres et al., 2006, 2009; Royo-Torres and Upchurch, 2012), that also involves, in some phylogenetic analyses, to *Galveosaurus* (e.g. Royo-Torres et al., 2006, 2012; Royo-Torres and Upchurch, 2012; Mocho et al., 2014a), which lacks most of the anterior caudal vertebrae. *Zby atlanticus* also related to Turiasauria, do not preserve caudal vertebrae (Mateus et al. 2014). The caudal vertebrae of *Losillasaurus* are similar to that of SHN 530, MNHN/UL.Din.027 and MMPM.P/73. The preserved vertebra of the Puntal de Santa Cruz (Royo-Torres et al., 2009) and some vertebrae of RD-13 (Cobos et al., 2011) also shares with SHN 180 a simple caudal rib and a slight convex posterior articulation, and probably, they occupy a more posterior position in the tail than SHN 530, MNHN/UL.Din.027 and MMPM.P/73.

Royo-Torres and Cobos (2005) described a slight procoelous vertebra from the Villar del Arzobisbo Formation (Tithonian-Berriasian) at Riodeva (Teruel) that was tentatively related to an indeterminate eusauropod. This vertebra probably corresponds to one of the first caudal vertebrae of the tail with a well-developed caudal rib. The presence of a longitudinal keel on the ventral face distinguishes this vertebra from *Losillasaurus* (Casanovas et al. 2001) and the Portuguese specimens.

Some anterior caudal vertebrae from the Iberian Peninsula could be assigned to Diplodocidae. From the fossil site of *Dinheirosaurus* holotype there are some fragments of anterior caudal vertebrae related with the same individual (Mannion et al., 2012), nevertheless, only the anterior part of a caudal centrum are published (Mannion et al., 2012). It is not so far possible to test the presence of the procoelous condition in this taxon. Other fragment with unknown locality housed in the collections of the Museu Municipal de Bombarral (MMB.PALEO.1), previously assigned to a theropod dinosaur (Mateus, 2005), could be assigned to a diplodocid. MMB.PALEO.1 presents a very slight procoelous posterior articular face and transversely concave ventral face with associated ventrolateral crests. Royo-Torres et al. (2007) also described a procoelous anterior caudal vertebra from Villar del Arzobispo sediments outcropping in El Carrillejo (Teruel, Spain). This vertebra (RD-11-1) also presents a slight procoelous condition, but the presence of wing-like processes, a ventral hollow and pleurocoels on lateral faces relate this specimen to Diplodocinae (Royo-Torres et al., 2007).

MG 4799 is a classical specimen housed in Museu Geológico collections (Lisboa, Portugal) found in the Upper Jurassic of Castanheira (Vila Franca de Xira, Portugal). The specimen was originally referred as a metatarsal V of *Apatosaurus alenquerensis* (Lapparent and Zbyszewski 1957). In a recent revision of this specimen, Mannion et al. (2013a) considered it as a procoelous caudal vertebra. Nevertheless, MG 4799 is interpreted herein as a right lateral side of an opisthocoelous dorsal vertebra.

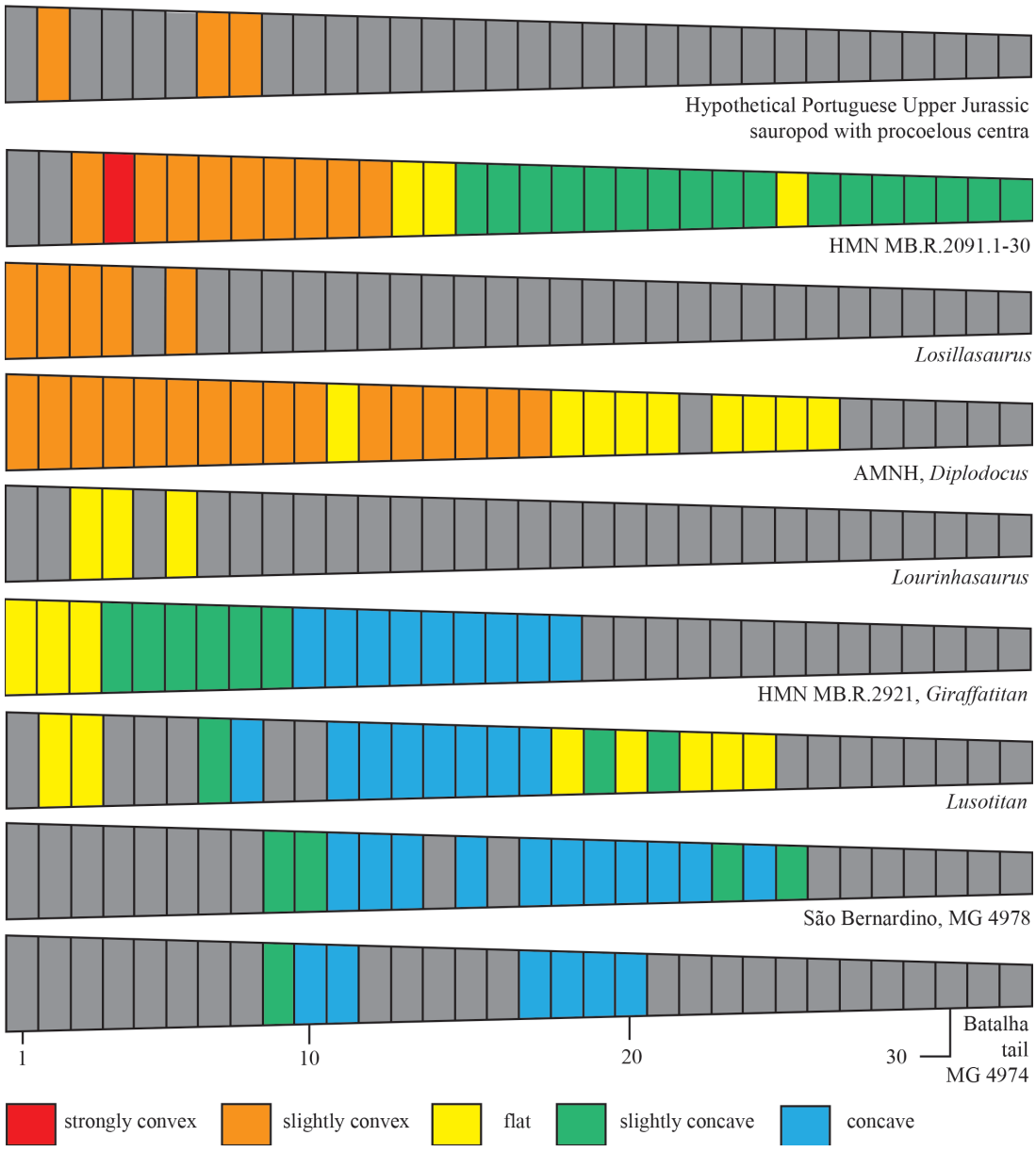

Figure 9.7. Evolution of the posterior articulation morphology along the tail in some caudal series collected in the Portuguese Upper Jurassic and other Upper Jurassic sauropods such as *Losillasaurus giganteus* (Casanovas et al., 2001), *Diplodocus* (AMNH 223, Osborn, 1904), HMN MB.R.2091.1-30 (Bonaparte et al., 2000).

In the Portuguese Upper Jurassic is possible to recognize four different morphotypes concerning to the anterior caudal vertebrae. The two morphotypes with procoelous condition are: *i*) diplodocid caudal vertebrae featured by the presence of pleurocoels, transversely concave ventral face and anteroposteriorly compressed neural spines as occur in *Dinheirosaurus* (Mannion et al., 2012; Royo-Torres et al., 2007; pers. observ., PM) and *ii*) anterior procoelous caudal vertebrae with convex ventral face, a convex posterior articulation with a local concavity and fan-like caudal

ribs with smooth prcdf, common in basal eusauropods such as *Losillasaurus* (Casanovas et al., 2011). In diplodocids, the procoelous condition might be present up to the middle/posterior caudal vertebrae transiting from a slight procoelous condition to a flat posterior articulation (Fig. 9.7; Osborn, 1899; Hatcher 1901; Gilmore 1936). The second morphotype is present in *Losillasaurus*, but the extension of the procoelous condition on the tail is unknown for this taxon (Fig. 9.7; Casanovas et al., 2001).

The anterior caudal vertebrae of *Lourinhasaurus* and *Lusotitan* represent two other morphotypes. *Lourinhasaurus* anterior caudal vertebrae bear a concave anterior articular face and flat posterior one. In *Lourinhasaurus*, the flat posterior articular face is present up to the 5th/6th caudal centrum (Fig. 9.7). In *Lourinhasaurus* the neural arch bears a circular sprf, delta-shaped neural spines and deep cprf (Fig. 9.6s-x; Mocho et al., 2014a). *Lusotitan* presents anterior concave articular faces and flat posterior ones as in *Lourinhasaurus*. At the level of the 7th/8th caudal centrum the posterior face is concave up to the 18th caudal vertebrae, in which the posterior articular face assume a flat morphology. The preserved anterior caudal rib is compressed anteroposteriorly with convex dorsal margin, considered as autamoporphic of this taxon (Fig. 9.6y-dd, Mannion et al., 2013a). In *Lusotitan*, the neural spine lacks a circular sprf as in *Lourinhasaurus*. The prcdf is not totally preserved in *Lusotitan* (Mannion et al., 2013a) but is smoother in most anterior caudals of this taxon. Two other partial tails were recovered from the Upper Jurassic sediments of the Lusitanian Basin. One of them is an anterior/middle caudal series (MG 4978) from São Bernardido at the Praia de Amoreira-Porto Novo Formation (Lapparent and Zbyszewski, 1957; Antunes and Mateus, 2003). In MG 4978, the posterior articular face presents a similar morphological pattern along the tail when compared with *Lusotitan* and *Giraffatitan* (Fig. 9.7; Janensch, 1950; Mannion et al., 2013a), nevertheless, the most anterior caudals are not preserved in this specimen, and no flat posterior articulations are recorded as in the recovered most posterior caudal centra. Another partial tail was collected in Batalha (MG 4974) that also has no significant differences in the morphology of the posterior articular face when compared with *Lusotitan*, MG 4978 and *Giraffatitan* (Fig. 9.7).

9.7. CONCLUSIONS

SHN 180, 530, MNHN/UL.Din.027 and MMPM.P/73 are the first references for the presence of procoelous caudal vertebrae of sauropods in the Upper Jurassic of the Lusitanian Basin (not considering a misidentified remain). The combination of slight procoelous centra, fan-shaped caudal ribs with smooth prcdf allows relating the described specimens to Eusauropoda, probably basal Eusauropoda. None of these vertebrae share several anatomical traits characteristic of the neosauropod groups with procoelous caudal vertebrae such as diplodocoids (wing-like transverse processes, deep pleurocoels, transversely concave ventral face plus lateroventral crest, transversely expanded neural spines, and contact between spol and sprl) or titanosaurs (transversely concave ventral face plus lateroventral crest, strongly procoelous centra and well developed cingulum in the posterior articulation). The absence of strong procoelous centra also suggests that the Portuguese specimens might not to be a member of Mamenchisauridae. The relationship of the Portuguese specimens with Turiasauria clade is not ruled out. SHN 530, 180, MNHN/UL.Din.027 and MMPM.P/73 share a similar morphology with the preserved anterior caudal vertebrae of *Losillasaurus*. On the other hand, SHN 180 has a similar morphology that the caudal vertebrae of the turiasaurs from Spanish localities of the Puntal de Santa Cruz and San Lorenzo. SHN 180, 530, MNHN/UL.Din.027 and MMPM.P/73 are confidently discernable from other anterior caudal vertebral morphotypes present in the Lusitanian Basin Upper Jurassic such as those of *Lusotitan* and *Lourinhasaurus*. The presence of this up to now unrecorded anterior caudal vertebral morphotype at the Portuguese Upper Jurassic is in accordance with the presence of turiasaurs in the Iberian Upper Jurassic. Nevertheless, the assignation to this clade can be not confirmed due to the absence of a diagnostic set of features related to the morphology of the anterior caudal vertebra.

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9.9. REFERENCES

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CHAPTER 10

Phylogenetic reassessment of *Lourinhasaurus alenquerensis*, a basal Macronaria (Sauropoda) from the Upper Jurassic of Portugal

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Phylogenetic reassessment of *Lourinhasaurus alenquerensis*, a basal Macronaria (Sauropoda) from the Upper Jurassic of Portugal

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Lourinhasaurus alenquerensis is a Portuguese Upper Jurassic dinosaur whose lectotype is one of the most complete sauropod specimens from the Portuguese fossil record and from the Upper Jurassic of Europe. It was recovered from sediments of the Sobral Formation (upper Kimmeridgian to lower Tithonian) at Moinho do Carmo (Alenquer, Portugal). The lectotype of *Lourinhasaurus* was first related to *Apatosaurus* and then tentatively related to *Camarasaurus*. Finally, it was established as a new taxon, *Lourinhasaurus*, including the Moinho do Carmo specimen. At the time of writing, *Lourinhasaurus* had a poor diagnosis and an unstable phylogenetic position. Revision of the Moinho do Carmo specimen has led to a detailed description and a new and more complete codification for several morphological characters. The phylogenetic analyses proposed herein considered *Lourinhasaurus* as a Camarasauromorpha Macronaria. This study also recovered a Camarasauridae clade incorporating *Lourinhasaurus*, *Camarasaurus* and, putatively, *Tehuelchesaurus* and that implies the presence of Camarasauridae in the European Upper Jurassic. Besides the strong similarity to *Camarasaurus*, *Lourinhasaurus alenquerensis* is here considered a valid taxon with 13 putative autapomorphies such as a sagittal keel on the dorsal margin of sacral neural spines, circular and deep spinoprezygapophyseal fossa on proximal caudal vertebrae, marked crest and groove bordering the lateral margin of the acetabulum in the ischium, and a marked deflection of the entire femoral shaft without lateral bulge. The apparently high number of taxa among the sauropod fauna from the Iberian Peninsula during the Late Jurassic is similar to the palaeobiodiversity recorded in formations of the same age, i.e. Morrison and Tendaguru, and does not support the hypothesis of a connection between the North America and Iberian Peninsula faunas during the later part of the Late Jurassic reflected by other faunal and floral groups.

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ADDITIONAL KEYWORDS: Alenquer – Camarasauridae – Camarasauromorpha – *Camarasaurus* – Lusitanian basin – phylogeny.

INTRODUCTION

The sauropods are one of the better represented vertebrate groups in the Kimmeridgian–Tithonian beds of the Portuguese Lusitanian Basin. Recent studies have suggested that these sauropod fauna are represented by exclusive taxa (Dantas *et al*., 1998; Bonaparte & Mateus, 1999; Antunes & Mateus, 2003; Royo-Torres, Cobos & Alcalá, 2006; Mannion *et al*., 2012, 2013) that are related to groups widely represented in the Upper Jurassic of other continents, such as brachiosaurids and diplodocids (Upchurch, Barrett & Dodson, 2004; Carballido *et al*., 2011; Whitlock,

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2011; D'Emic, 2012; Mannion *et al*., 2013). Sauropod fauna from the Portuguese Upper Jurassic comprise three taxa: *Lourinhasaurus alenquerensis* (Lapparent & Zbyszewski, 1957), *Dinheirosaurus lourinhanensis* Bonaparte & Mateus (1999), and *Lusotitan atalaiensis* (Lapparent & Zbyszewski, 1957). Other specimens of Portuguese Upper Jurassic sauropods have been related to Turiasauria (Royo-Torres *et al*., 2006, 2009; Mateus, 2009; Ortega *et al*., 2010; Mocho, Ortega & Royo-Torres, 2012), basal Macronaria (Yagüe *et al*., 2006), and a putative second diplodocid (Mannion *et al*., 2012).

The *Lourinhasaurus* type site was discovered by the North American geologist Harold Weston Robbins during his employment with the Portuguese Petroleum Company; the site lies at the northern end of a ruined windmill named Moinho do Carmo (Lapparent & Zbyszewski, 1957). Lapparent & Zbyszewski (1957) indicated that fieldwork was carried out by the Serviços Geológicos de Portugal in June 1949 under the direction of the geologist Georges Zbyszewski.

The Moinho do Carmo specimen, along with other fragmentary specimens, was related to *Apatosaurus* by Lapparent & Zbyszewski (1957) because it shares the following characteristics with this taxon: (1) strength of cervical vertebrae; (2) development of cervical ribs; (3) massive and elevated middle caudal vertebrae; (4) short forelimbs compared with hindlimbs; and (5) a large and very massive pubis. The ratio between forelimb and hindlimb length, elongation of astragalus, robustness of the pelvis ,and dimensions of cervical ribs were used by these authors to define a novel species, *Apatosaurus alenquerensis*. This taxonomic attribution was maintained by Steel (1970).

McIntosh (1990a, b) and McIntosh *et al*. (1996b) proposed a new taxonomic framework for the Moinho do Carmo specimen. These authors noted similarities between this material and *Camarasaurus*, including the presence of 12 dorsal vertebrae (all of them opisthocoelous), a broadly expanded distal end of the scapula, a long slender humerus, and an unexpanded distal end of the ischium. They proposed a provisory assignation of the specimen as ?*Camarasaurus alenquerensis.* This taxonomic assignation was supported by Wilson & Sereno (1998). Indeed, McIntosh (1990b) and McIntosh *et al*. (1996b) suggest the possibility of naming a new genus for this material on the basis of its higher humerus to femur length ratio compared with *Camarasaurus*, but they considered that more material, in particular neurapophyses or cranial remains, is necessary to support this.

Dantas *et al*. (1998) defined *Lourinhasaurus* after combining the information from the Moinho do Carmo specimen with a new finding (cervical and dorsal series vertebrae) from Porto Dinheiro (Lourinhã) [Dantas *et al*. (1992)]. These authors proposed a diagnosis for *Lourinhasaurus* that was based almost exclusively on the Porto Dinheiro material. One year later, Bonaparte & Mateus (1999) reclassified the Porto Dinheiro specimen as representing a new diplodocid, *Dinheirosaurus lourinhanensis*; this assignation was recently supported by Mannion *et al*. (2012). Bonaparte & Mateus (1999) considered it impossible to compare the two specimens but accepted the validity of *Lourinhasaurus*, restricting it to the Moinho do Carmo material and other fragmentary specimens from Alcobaça, Areia Branca, Chiqueda de Cima, Foz de Arelho, Ourém, Porto das Barcas, Salir de Matos, Santa Cruz, São Bernardino, São Mamede, Torres Vedras, and Vale Frades (Antunes & Mateus, 2003). Antunes & Mateus (2003) related *Lourinhasaurus* to Macronaria and defined the Moinho do Carmo specimen as the lectotype of the species.

Previous phylogenetic hypotheses consider *Lourinhasaurus* as a basal eusauropod (Upchurch *et al*., 2004), as a basal macronarian (Royo-Torres *et al*., 2006; Barco, 2010), or as a neosauropod non-macronarian (Fig. 1) (Royo-Torres & Upchurch, 2012; Royo-Torres, Alcalá & Cobos, 2012). Royo-Torres (2009) and Royo-Torres *et al*. (2012) also consider the possibility that it represents a form that is related to Laurasiformes.

Another specimen from the Portuguese Upper Jurassic, collected from Peralta (lower Tithonian), was related to *Brachiosaurus* but with a new specific assignation, *Brachiosaurus atalaiensis* (Lapparent & Zbyszewski, 1957). Antunes & Mateus (2003) revised this material and established a new generic taxon, the basal macronarian *Lusotitan atalaiensis*, which they included, with doubt, in Brachiosauridae (Mannion *et al*., 2013).

Herein, we reassess the Moinho do Carmo classical material assigned to *Lourinhasaurus alenquerensis*, and the validity of this taxon, especially in comparison with contemporaneous sauropods, is discussed. An amended diagnosis is also formulated, and a phylogenetic hypothesis involving this taxon is proposed. Finally, the palaeobiogeographical implications of *Lourinhasaurus* for our understanding of the relationships of the fauna present in the proto-North Atlantic during the Late Jurassic are discussed.

GEOLOGICAL SETTING

The remains described herein were collected north of Lisbon, about 1.5 km south of Alcobaça, near a windmill ruins named 'Moinho do Carmo' (Fig. 2A, B). The sedimentary sequence outcropping in Moinho do Carmo fits in the Upper Jurassic to Lower Cretaceous sequence deposited in the Lusitanian Basin during the 3rd rifting episode (Rasmussen *et al*., 1998; Kullberg *et al*., 2006), a period marked by the internal

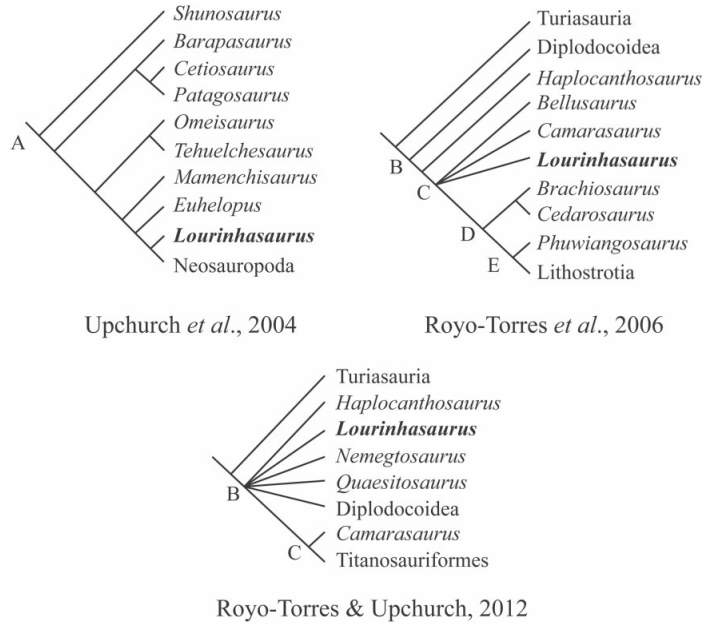

Figure 1. Previous phylogenetic hypotheses based on cladistic analysis approaches including *Lourinhasaurus*. A, Eusauropoda; B, Neosauropoda; C, Macronaria; D, Titanosauriformes; E, Titanosauria.

differentiation of the basin into several sub-basins and resulting in an important siliciclastic input that progressively infilled these basins (Pena dos Reis *et al*., 2000). Above the Kimmeridgian, the sedimentary sequence is strongly siliciclastic with a continental signature at the top of the sequence (Hill, 1988).

The Moinho do Carmo quarry is located in the Arruda sub-basin (Guéry, 1984) and the outcropping sediments were referred as the 'Complexo pteroceriano incluindo as camadas com Lima pseudoalternicosta' by Zbyszewski & Torre de Assunção (1965), and more recently considered to belong to the Farta Pão Formation (Leinfelder & Wilson, 1989). Schneider, Fürsich & Werner (2009) included as members of the Farta Pão Formation the previous Sobral, Arranhó (divided into the Arranhó I and II members), and Freixial Formations. *Lourinhasaurus alenquerensis* material was collected from red and grey mudstone intercalated by yellow sandstones and white limestone with pisolites (Lapparent & Zbyszewski, 1957) of the Sobral Member (Fig. 2C; Ribeiro & Mateus, 2012). The Sobral Member or Formation (e.g. Leinfelder, 1993; Kullberg *et al*., 2006; Schneider *et al*., 2009) is interpreted as an estuarine delta complex (Leinfelder, 1993; Kullberg *et al*., 2006) dated to the late Kimmeridgian to early Tithonian (Fürsich, 1981). The Sobral Formation/Member has yielded a rich vertebrae fossil assemblage highlighting the type specimens of the titanosauriform *Lusotitan atalaiensis* (Lapparent & Zbyszewski, 1957) and the theropod *Lourinhanosaurus antunesi* Mateus, 1998.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; MG LNEG, Museu Geológico do Laboratório Nacional de Energia e Geologia, Lisbon, Portugal; USNM, United States National Museum, Washington, DC, USA.

Anatomical abbreviations

acr, acromial crest; acdl, anterior centrodiapophyseal lamina; acet, acetabulum; acpl, anterior centroparapophyseal lamina; al, accessory lamina; asp, ascending process; aspa, articular surface for ascending process; at, anterior trochanter; cap, capitulum; cc, cnemial crest; cdf, centrodiapophyseal fossa; cof, coracoidal foramen; cpol, centropostzygapophyseal lamina; cprl, centroprezygapophyseal lamina; d, diapophysis; das, distal articular surface; dpc, deltopectoral crest; eprl, epipophyseal–prezygapophyseal lamina; fia, fibular articular surface; fic, fibular condyle; ft,

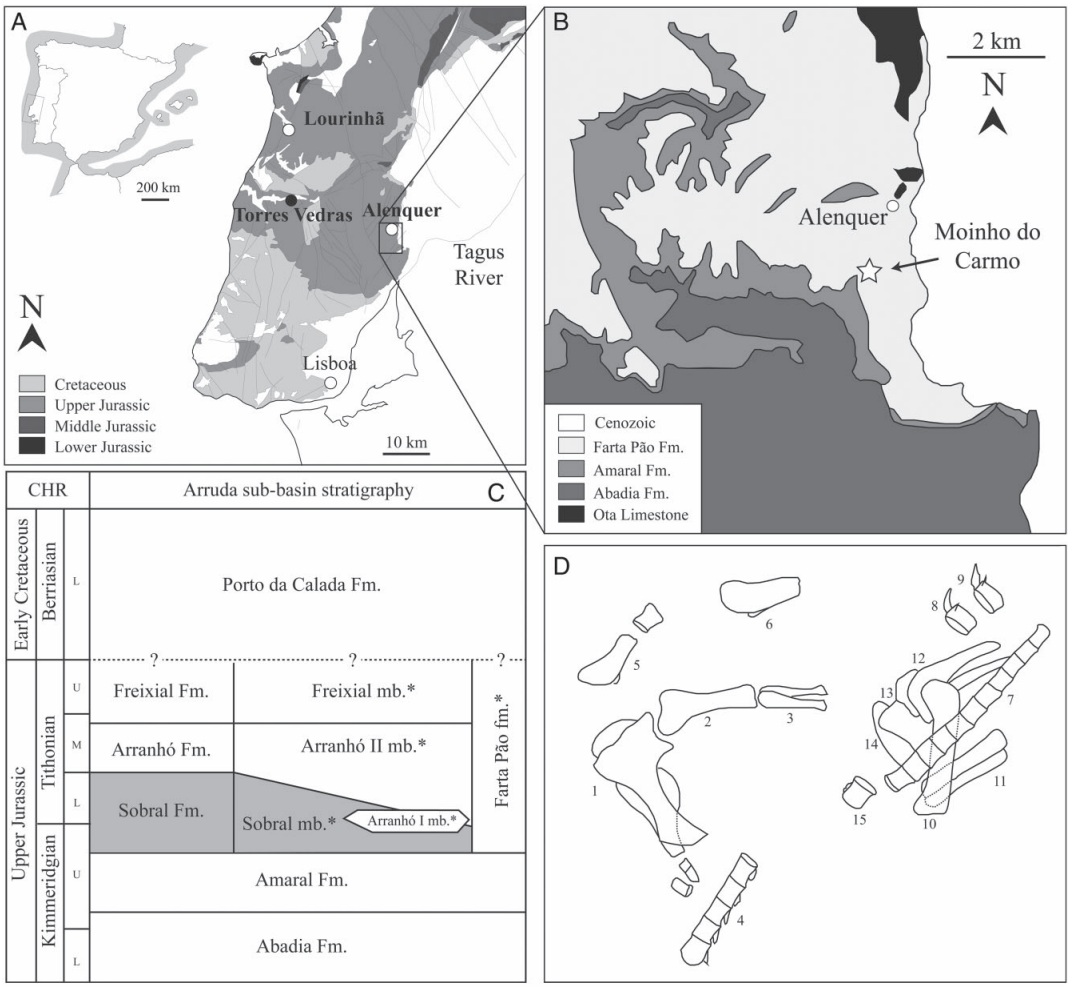

Figure 2. A, geological map (adapted from Oliveira *et al*., 1992) showing the Portuguese Mesozoic levels. B, geological map of the Alenquer region (adapted from Leinfelder & Wilson, 1989) with the location of the Moinho do Carmo site. C, stratigraphy of Arruda sub-basin *sensu* Kullberg *et al*. (2006) (**sensu* Schneider *et al*., 2009, 2010); CHR, chronostratigraphy. D, Moinho do Carmo quarry map (adapted from Lapparent & Zbyszewski, 1957) and its interpretation: 1, scapulae girdle; 2, left humerus; 3, left radius and ulna; 4, cranial-to-middle dorsal vertebrae (DV1 to DV5); 5, right humerus; 6, sternal plates (?); 7, middle dorsal-to-sacral vertebrae (DV7 to DV12 and the sacral centra); 8 and 9, proximal caudal vertebrae; 10, left femur; 11, left tibia, fibula and astragalus; 12, ischia; 13, pubis; 14, left ilium; 15, middle dorsal vertebrae (DV6).

fourth trochanter; gl, glenoid; ilped, iliac peduncle; lep, lateral epicondyle; lt, lateral trochanter; of, obturator foramen; isped, ischial peduncle; pa, parapophysis; pacdf, parapophyseal centrodiapophyseal fossa; paf, posterior astragalar fossa; pafc, crest in posterior astragalar fossa; pas, proximal articular surface; pcdl, posterior centrodiapophyseal laminae; pcpl, posterior centroparapophyseal lamina; pl, pleurocoel; pocdf, postzygapophyseal centrodiapophyseal fossa; podl, postzygodiapophyseal lamina; poap, postacetabular process; posdf, postzygapophyseal spinodiapophyseal fossa; ppdl, paradiapophyseal lamina; pped, pubic peduncle; prap, preacetabular process; prcdf, prezygapophyseal centrodiapophyseal fossa; prdl,

prezygodiapophyseal lamina; prep, prespinal process; prsl, prespinal lamina; prpl, prezygoparapophyseal lamina; pvp, posteroventral process; rac, radial condyle; sdf, spinodiapophyseal fossa; spdl, spinodiapophyseal lamina; spol, spinopostzygapophyseal lamina; spof, spinopostzygapophyseal fossa; sprl, spinoprezygapophyseal lamina, sprf, spinoprezygapophyseal fossa; tia, tibial articulation; tic, tibial condyle; tp, transverse process (sacral rib or caudal rib, *sensu* Wilson, 2011); ulc, ulnar condyle; ucp, ulnar cranial process; uclp, ulnar craniolateral process; vpr, ventral process.

Terminology

The terminology applied for vertebrae laminae and fossae follows Wilson (1999, 2012) and Wilson *et al*. (2011), respectively. The nomenclature applied in the descriptions of *Lourinhasaurus* bones also follows Wilson & Sereno (1998) and the elements are orientated *sensu* Upchurch *et al*. (2004).

SYSTEMATIC PALAEONTOLOGY

Dinosauria Owen, 1841

Saurischia Seeley, 1887

Sauropoda Marsh, 1878

Neosauropoda Bonaparte, 1986

Macronaria Wilson & Sereno, 1998

Camarasauromorpha Salgado, Coria & Calvo, 1997

Camarasauridae Cope, 1877

Lourinhasaurus Dantas *et al*., 1998

Type species: Lourinhasaurus alenquerensis (Lapparent & Zbyszewski, 1957)

Diagnosis: See diagnosis for type and only species below.

Lourinhasaurus alenquerensis (Lapparent & Zbyszewski, 1957)

1957 *Apatosaurus alenquerensis* Lapparent & Zbyszewski, 1957

1990a ?*Camarasaurus alenquerensis* McIntosh, 1990a

1990b ?*Camarasaurus alenquerensis* McIntosh, 1990b

1996b ?*Camarasaurus alenquerensis* McIntosh *et al*. 1996b

1998 *Lourinhasaurus alenquerensis* Dantas *et al*. 1998

2003 *Lourinhasaurus alenquerensis* Antunes & Mateus, 2003

Lectotype: Partial skeleton (Fig. 2D) housed in MG LNEG composed by: cervical vertebrae remains (MG4956, MG30373, MG30377, and MG30379), 12 dorsal vertebrae and several neurapophyses fragments (MG4956: 11 dorsal centra; MG30378: the cranialmost dorsal centra; MG30384: neurapophyses fragments), several cranial-to-caudal dorsal ribs (MG30370), five sacral vertebrae (MG4956), sacral ribs (MG30380)* and three sacral neural spines (MG30376)*, three proximal vertebrae and two proximal caudal neurapophyses (MG4956, MG30374, MG30388), chevron fragments (MG30387)*, left (MG 5780) and right (MG30371) scapulae, left (MG5780) and right (MG30372) coracoids, left (MG30383) and right (MG30382) sternal plates*; left (MG2) and right (MG30381) humeri, left radius (MG4979), left ulna (MG4979), carpal II (MG30385), left ilium (MG5781), right (MG4975) and left (MG4970) pubis, left and right ischia (MG4957), left femur (MG4931), left tibia (MG4983), left fibula (MG4984), left astragalus (MG30375), pedal (?) phalanx 2 (MG30386)* and other several indeterminate fragments without explicit acronyms. All these elements are labelled and related to a unique individual, but some elements (marked with an asterisk) were not explicitly referred to in the original description (Lapparent & Zbyszewski, 1957); and there are some elements, originally quoted by these authors, that cannot be recognized in the available set of elements.

Emended diagnosis: Macronarian having the following autapomorphies: (1) cranial-to-middle dorsal vertebrae with transversely concave ventral face bounded by longitudinal smooth crests; (2) sagittal keel in dorsal margin of sacral neural spines; (3) when the sacral neural spines are vertical becomes significantly higher caudally, and the dorsal margin bears a marked cranial slope; (4) prespinal process with a sagittal lamina (prespinal lamina) in the dorsal sector of the sacral spine subdividing a smooth prespinal fossa; (5) circular and deep spinoprezygapophyseal fossa on proximal caudals (also shared by *Jobaria*); (6) the dorsal surface of the most proximal caudal spine slopes cranially transiting continuously to the cranial face of the spine, and the caudal edge produces a transverse hooked-like process in lateral view; (7) circular process on distal surface of carpal II; (8) longitudinal crest in ventral margin of ilium postacetabular process near ischiatic peduncle; (9) caudal orientation of the postacetabular process with the chord through the ischiatic and pubic articulations passing through ventral margin of the postacetabular process; (10) axis of pubic peduncle and ischiatic articulation parallel; (11) marked crest and groove bordering the lateral margin of acetabulum in the ischium; (12) tibia and fibula of equal

length, implying a more distal position of the fibula relative to the tibia for the reception of the astragalus; (13) marked deflection of the entire femoral shaft without lateral bulge.

Etymology: Lourinhasaurus, *Lourinha*, from Lourinhã, a municipality north of Lisbon where one of the specimens related to this taxon was found (Dantas *et al*., 1998), later considered as the holotype of *Dinheirosaurus lourinhanensis* (Bonaparte & Mateus, 1999); *saurus*, greek for lizard; and *alenquerensis*, from Alenquer, a municipality north of Lisbon where the lectotype specimen of the taxon was found.

Horizon and locality of the lectotype: Moinho do Carmo, Alenquer municipality, north of Lisbon, Sobral Formation (or Sobral Member of the Farta Pão Formation *sensu* Schneider *et al*., 2009), upper Kimmeridgian to lower Tithonian, Lusitanian Basin.

DESCRIPTION

Axial skeleton

Cervical vertebrae: A cranial-to-middle (MG30377, Fig. 3A, B) and a middle-to-caudal (MG30373, Fig. 3C, D) cervical vertebra as well as several fragments (e.g. MG4956) were identified. The most complete centrum (slightly fractured caudally, MG30373) is transversely constricted in the middle sector and shows an elongation index (*sensu* Upchurch, 1998) of 1.8. The ventral face is flat to slightly concave and is limited by marked lateral margins resembling crests (Fig. 3D). The pleurocoels are deep, occupying most of the length of the centrum, and are separated by a 20-mm-thick sagittal plate. Each pleurocoel is laterally divided by at least one vertical lamina, creating two main cavities. Internally, the pleurocoels are divided into several cavities. Considering the morphological categories defined by Wedel, Cifelli & Sanders (2000), the cervical vertebrae of *Lourinhasaurus* bears polycamerate pneumaticity.

MG30377 (Fig. 3A, B) and a caudal cervical neurapophysis lacking the distal portion of the spine and the parapophyses, pre- and postzygapophyseal processes (MG30379, Fig. 4), were identified. In MG30377, the neurapophysis is displaced and slightly rotated relative to its original position. In lateral view, dorsal to the pleurocoel margin, there is a marked posterior centrodiapophyseal lamina (pcdl) that has an arched profile and slopes latero-ventrally. In MG30377, below the pcdl, there is a centrodiapophyseal fossa (cdf) that is subdivided into two smooth subfossae. These subfossae are considered homologous to two deep circular foramina below the pcdl present in MG30379, and in the later

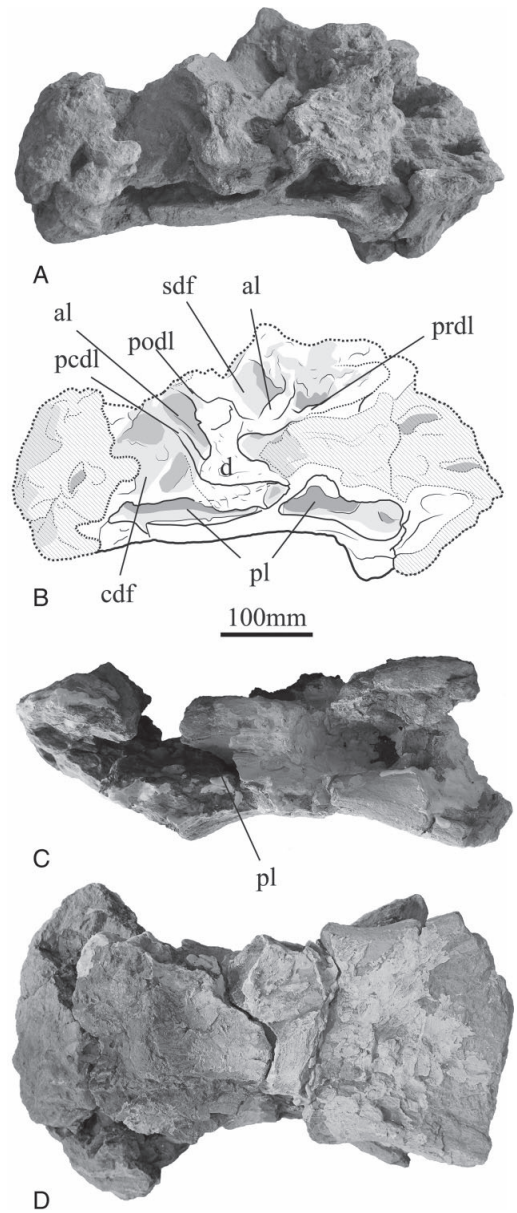

Figure 3. Cervical vertebrae of *L. alenquerensis*. Cranial-to-middle cervical centrum (MG30377) in right view (A) and its schematic interpretation (B); middle-to caudal cervical centrum (MG30373) in left (C) and ventral (D) view. Traced line: broken borders; fill in traced pinstripes: broken or eroded areas.

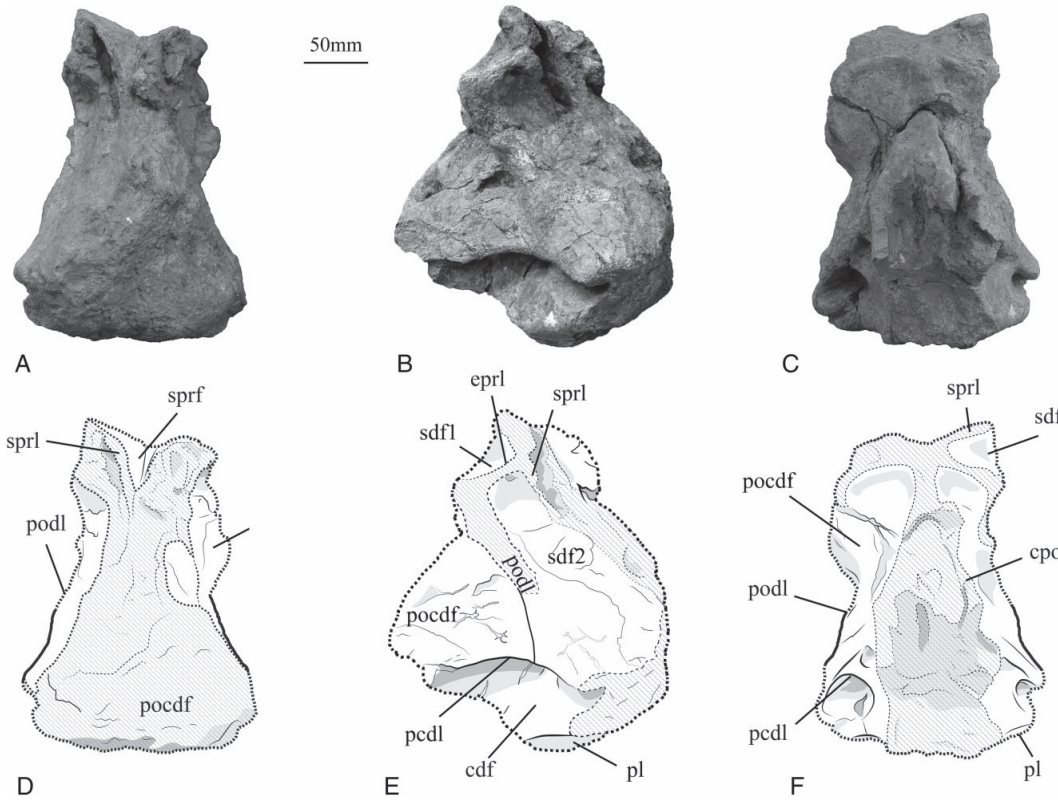

Figure 4. Partial neural arch of caudal cervical vertebra of *L. alenquerensis* (MG30379) in cranial (A), right lateral (B), and caudal (C) views and their respective interpretations (D, E, F). Traced line: broken borders; fill in traced pinstripes: broken or eroded areas.

element (MG30377) being separated by a stout vertical accessory lamina emerging from the pcdl. In the most cranial vertebrae (MG30377), the postzygodiapophyseal lamina (podl) emerges from the diapophysis, whereas in the caudalmost cervical neurapophyses (MG30379) this lamina has a more caudal position, emerging from the pcdl at an angle of 45°. The podl is smoother in MG30379, becoming more prominent caudally. The pcdl and podl border a subtriangular postzygapophyseal centrodiapophyseal fossa (pocdf) that consists of two sectors, a cranial sector facing laterally and a caudal sector facing more caudolaterally to which the cranial sector progressively transits. In the most cranial cervical vertebra (MG30377), there is a smooth accessory lamina between the pcdl and the podl that emerges from the diapophysis and is orientated parallel to the pcdl. In caudal view, the pocdf displays a smooth subfossa in its dorsal sector.

In MG30379, the podl bifurcates into two laminae, a cranial and subhorizontal lamina that is interpreted as the epipophyseal–prezygapophyseal lamina (eprl) and a caudal and subhorizontal lamina that is the caudal continuation of the podl toward the postzygapophyses (this sector is not preserved in the most cranial vertebrae). The eprl divides the sector above the diapophysis into two fossae, the dorsal spinodiapophyseal fossa 1 (sdf1), which is bordered at least by the eprl and the podl, and the ventral spinodiapophyseal fossa 2 (sdf2), which is located cranially to the podl and is bordered dorsally at least by the eprl. In a lateral view of MG30377, unlike in MG30379, there is no subdivision of the sdf. In MG30377, it is possible to recognize two other laminae, the prezygodiapophyseal lamina (prdl) and an accessory vertical lamina that emerges from the prdl and divides the sdf into two fossae. This accessory lamina emerges from prdl and is craniodorsally

developed being considered non-homologous of the eprl observed in MG30379. The eprl is a lamina that connects the epipophyses to the prezygapophyses (Wilson, 2012). Therefore, the two subfossae observed in the sdf are not considered homologous to sdf1 and sdf2 in the most caudal cervical spine.

The cranial and caudal sectors of both cervical neurapophyses are not well preserved. In cranial view, one can observe the presence of a spinoprezygapophyseal fossa (sprf) with a smooth surface limited by the spinoprezygapophyseal laminae (sprl) that diverge laterally.

Dorsal vertebrae: Herein, on the basis of the pictures and quarry map in Lapparent & Zbyszewski (1957), the relative positions of the 12 preserved dorsal centra are tentatively assigned (Fig. 5). The total number of dorsal vertebrae is unknown for this specimen. Each centrum is described by its relative position, from cranialmost (DV1) to caudalmost (DV12) centrum. Because the centra show strong and variable deformation, it is difficult to obtain reliable values for the elongation index (EI). The least-deformed centrum (DV10) has an EI of 1.12. Every dorsal centrum is strongly opisthocoelous and has a central circular depression in the cranial articulation. The centra are transversely constricted at midlength and have transverse subcircular outlines (Fig. 6A–C). The centra from DV3 to DV6 bear a craniocaudal concavity along their ventral faces, a feature that is considered an autapomorphy of *Lourinhasaurus alenquerensis* (Figs 5, 6D). In DV5, this concavity is restricted to the cranial sector of the ventral face. The craniocaudal concavities are laterally limited by

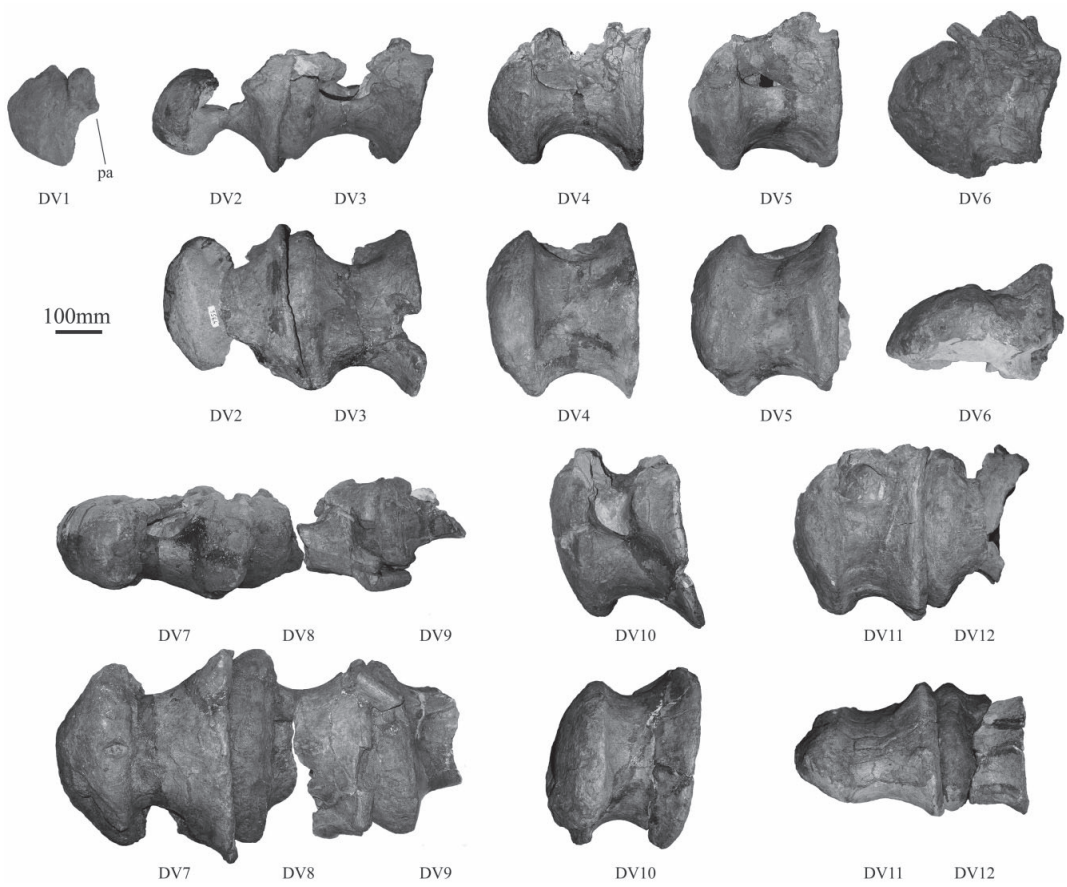

Figure 5. Dorsal vertebrae series of *L. alenquerensis* (MG4956 and MG30378) in left (first and third lines) and ventral (second and fourth lines) views.

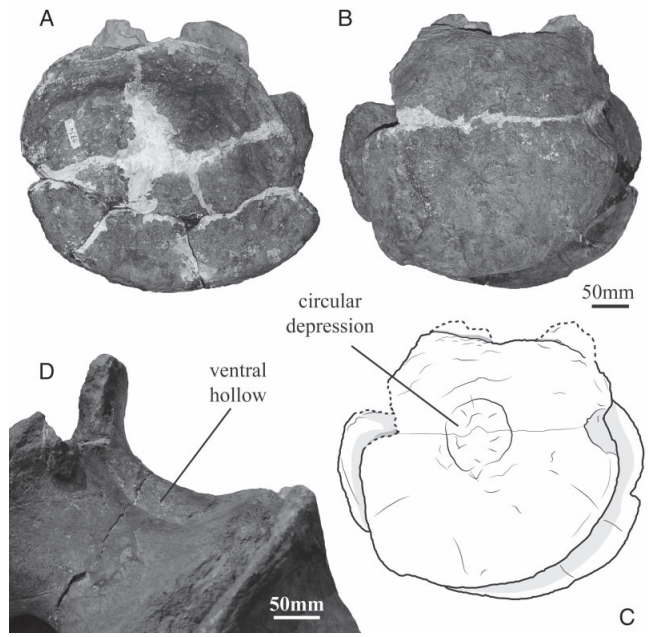

Figure 6. Caudal dorsal vertebrae DV10 (MG4956) of *L. alenquerensis* in caudal (A) and cranial (B) views and its schematic figuration (C) showing the circular depression on the cranial articular surface. Ventral surface of the cranial dorsal vertebra DV3 (MG4956) bearing its ventral concavity (D), an autapomorphy of *L. alenquerensis*. Traced line: broken borders.

craniocaudal crests, producing a biconvex transverse outline of the centrum ventral face. In the DV2 and from the DV7–DV12 centra, the ventral face is slightly flat-to-convex and transits continuously toward the lateral face. In general, the radial length of the caudal face is larger than that of the cranial face. Every vertebra bears deep pleurocoels located craniodorsally on the lateral face of its centrum and occupying ½ to ⅔ of the lateral central length. The pleurocoels of the cranial dorsal centra have elliptical outlines that are compressed dorsoventrally and taper cranially and caudally, becoming progressively rounded and smaller toward the most caudal centra. The pleurocoels are ventrally expanded and are separated by a sagittal lamina 20 mm thick that is quite constant along the dorsal sequence. Cranially, the pleurocoels become deeper and more complex with few ramifications in the cranial and caudal zones of the centrum (Fig. 7). The dorsal vertebrae of *Lourinhasaurus* bear a polycamerate to camerate pneumaticity (*sensu* Wedel *et al*., 2000). The neural arches are placed cranially and do not occupy the caudal part of the dorsal face of the centrum. In the last preserved dorsal centra, DV11 and DV12, the neural arches occupy the entire craniocaudal extension.

The most cranial dorsal centrum preserves the left parapophysis and is located near the craniodorsal margin of the pleurocoel. Below the parapophysis, two laminae emerge from its caudoventral margin, a cranial subvertical lamina that slopes backwards and a medial subhorizontal caudal lamina. These laminae border the excavated region below and behind the parapophyses, displaying a subtriangular contour. The cranial subvertical lamina and the medial subhorizontal caudal lamina are probably homologous to the anterior centroparapophyseal lamina (acpl) and the posterior centroparapophyseal lamina (pcpl), respectively. This fossa probably communicates with the pleurocoel caudally or corresponds to a subdivision of the pleurocoel. Above the 'pcpl', there is a small subtriangular fossa. The parapophysis surface is excavated and has a transverse subrectangular outline.

Some remains of neurapophyses (DV6 – MG4956, in which the neurapophysis is collapsed, and MG30384 fragments) were identified and were assigned to middle centra (Fig. 8). On these fragments, it is possible to observe the presence of a stout acpl that bifurcates ventrally near the dorsal margin of the pleurocoel where the caudal branch reaches the caudoventral margin of the neural arch. Between the two

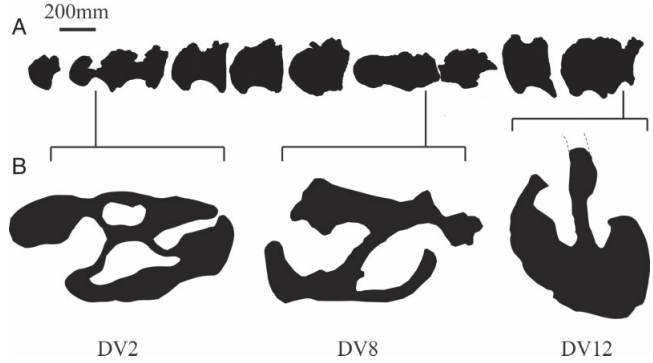

Figure 7. Change in the pneumaticity along the dorsal series of *L. alenquerensis*. Lateral view of the dorsal series (A) and the cross-section of DV2, DV8, and DV12 (B, without scale). The traced line indicates lost bone.

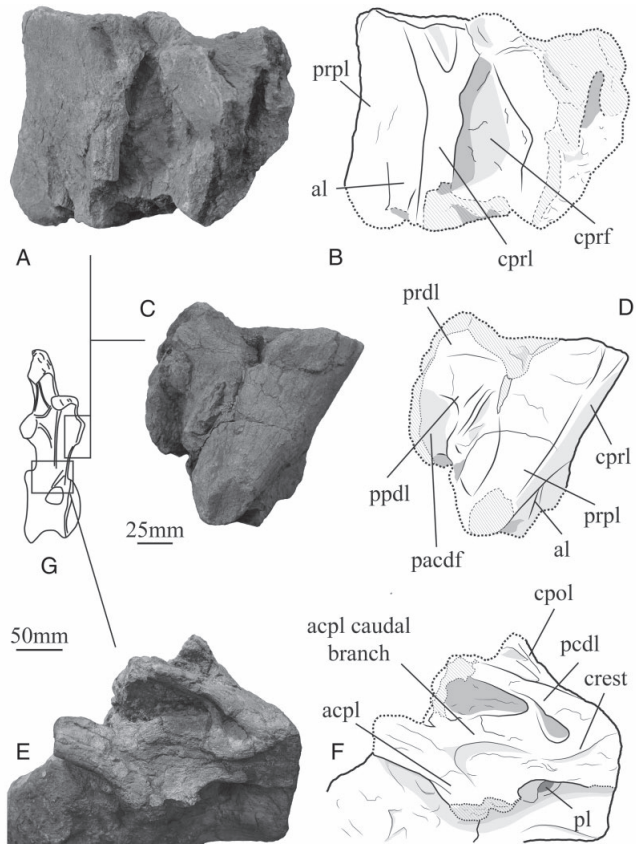

Figure 8. Middle neural spine of *L. alenquerensis* (probably from the 6th or 7th dorsal vertebra, MG30384) in cranial view (A) and its schematic interpretation (B); and in right view (C) and its schematic interpretation (D). Neural arch of *L. alenquerensis* DV6 in left view (E) and its schematic interpretation (F). Traced line, broken borders; fill in traced pinstripes, broken or eroded areas. G, *Camararasaurus* dorsal vertebrae (Osborn & Mook, 1921: pl. LXX) with boxes indicating the relative position of the figured *Lourinhasaurus* neural arch fragments.

branches of the acpl, there is a smooth fossa that lies craniodorsal to the pleurocoel. Caudal to the caudal branch of the acpl, a pcdl bifurcates ventrally into two branches that border a small but well-marked teardrop-shaped fossa. The caudal branch reaches as far as the caudal margin of the neurocentral junction. The acpl structure and pcdl limit another fossa, the parapophyseal centrodiapophyseal fossa (pacdf). A second cranially directed lamina is broken, and it is difficult to determine whether this lamina represents the ppdl.

The prezygapophyses are robust and are supported ventrally by a cprl and a prpl. The cprl is bifurcated dorsally close to the prezygapophyses. Between the cprl and the prpl, there is an accessory lamina (al), dorsoventrally developed, that begins considerably below the prezygapophysis. The preserved sector of the centroprezygapophyseal fossa (cprf) is deep and flat (DV6 – MG4956 and MG30384). The postzygapophyses are circular in contour, and their surfaces are flat to concave. The centropostzygapohyseal lamina (cpol) is columnar and delimits a shallow centropostzygapophyseal fossa (cpof).

The unique preserved neural spine is probably a fragment of the 6th or 7th dorsal spine (Fig. 9, MG30384), based on comparison with the dorsal series of *Camarasaurus* (e.g. Osborn & Mook, 1921). This spine is basally constricted and transversely expanded in the dorsal direction. The dorsal margin of the neural spine bears a sagittal concavity, laterally bounded by two small round rod-like dorsal processes 35 mm in height. Comparing several dorsal vertebrae series with non-bifid and bifid neural spines (e.g. Hatcher, 1901, 1903; Osborn & Mook, 1921; Janensch, 1929; Gilmore, 1936; Powell, 1992; McIntosh *et al*., 1996a, b; Tang *et al*., 2001; Ikejiri, 2004; Campos *et al*., 2005; McIntosh, 2005; Curry Rogers, 2009), the presence of a concavity in the dorsal margin corresponds to the transition between bifid and non-bifid neural spines. Laterally, these processes extend downward into the triangular rounded lateral process. The morphology of the spine in cranial or caudal view is roughly rhombus-like. The lateral boundary is probably an spol laminae tapering ventrally. The caudal surface is concave and rough. The cranial face is convex and broken in the prespinal area, lacking the prespinal process.

Dorsal ribs: Several distal to proximal fragments of dorsal ribs were identified. Only one caudal dorsal rib (a right one) preserves part of the capitulum and lacks the tuberculum in the proximal zone (Fig. 10A, B). All preserved dorsal ribs present a solid bone tissue. The caudal and the cranial face of proximal section are both concave and there is no sign of a pneumatopore in the caudal surface. The proximal sections of cranialmost ribs display a pronounced and laterally displaced crest (it probably meets with the tuberculum) on the cranial face and a concave caudal face. In cross-section those proximal sections show a 'T' outline (Fig. 10C). The middle and the distal sectors of the ribs are 'plank'-like bearing an elliptical cross-section (the craniocaudal length is three times the lateromedial length) in their distal portions.

Sacral vertebrae: The sacral region is composed of five fused vertebrae (Fig. 11A, B). The sacrum shows a slight curvature (convexity faces ventrally); consequently, the last sacral caudal articulation faces craniodorsally. The centra are as tall as they are long and are transversely constricted at midlength. Beneath the surface of the broken transverse

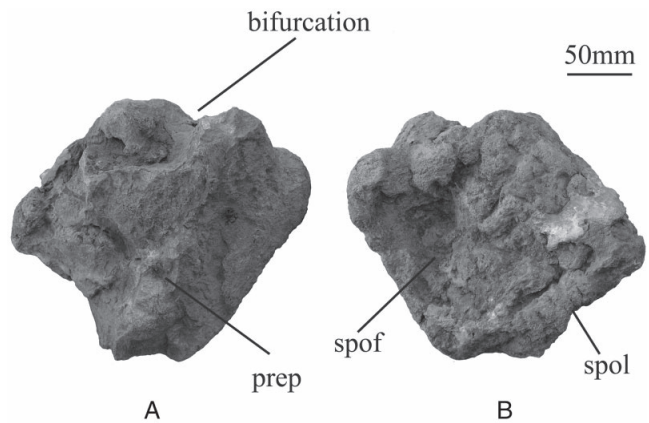

Figure 9. Fragment of a middle neural spine of *L. alenquerensis* in cranial (A) and caudal (B) views.

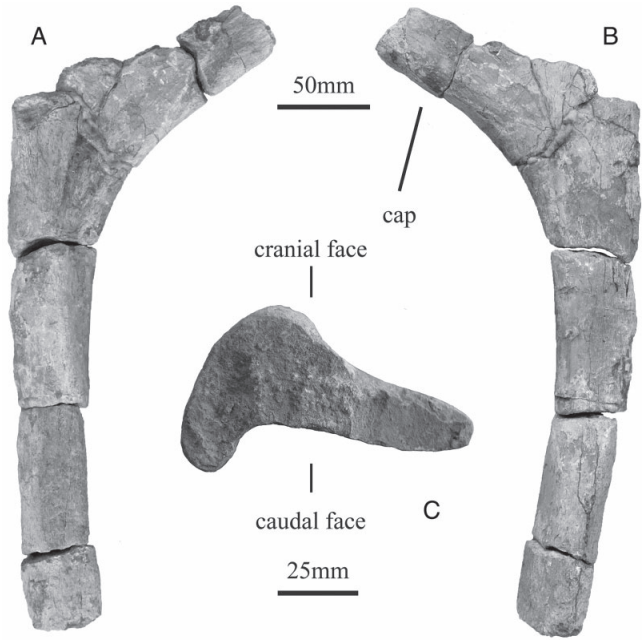

Figure 10. Dorsal rib of *L. alenquerensis* (MG30370). Proximal section of a caudal dorsal rib in caudal (A) and cranial (B) view; and the cross-section of a proximal-to-middle sector of cranial dorsal rib (C).

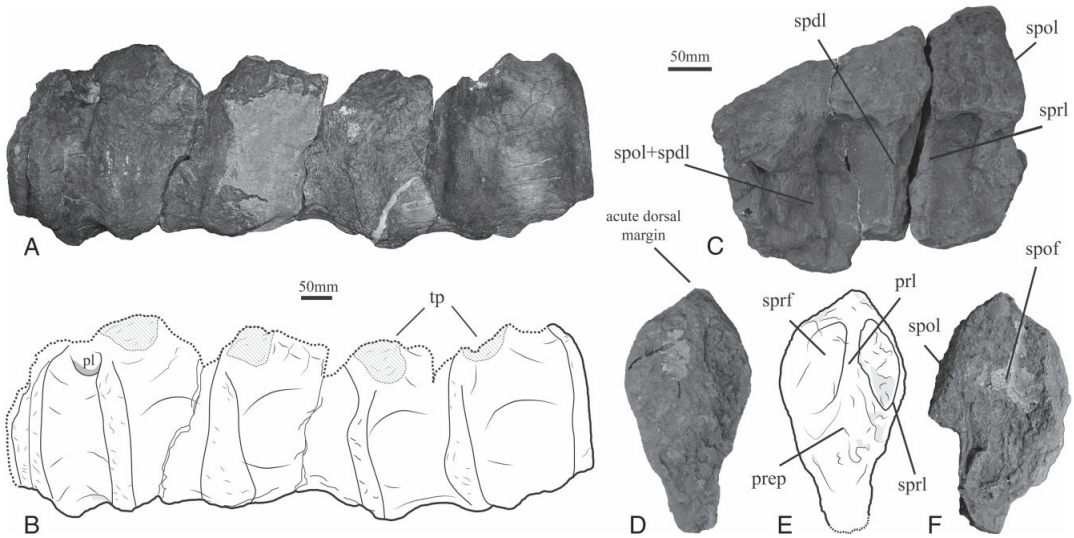

Figure 11. Sacral remains of *L. alenquerensis*. Sacral centra (MG4956) in left view (A) and its schematic interpretation (B). Sacral neural spines (MG30376): left view (C) and the most caudal available sacral spine in cranial view (D) with its schematic interpretation (E), and caudal view (F).

processes, a wide depression occupies much of the lateral face, but only the first sacral vertebra bears a true pleurocoel that is craniocaudally shorter than the dorsal pleurocoels. The lateral face of the centrum slopes medioventrally and passes continuously to the ventral face. The ventral face is mediolaterally narrow, as occurs in other sauropods such as *Tastavinsaurus* (Royo-Torres, 2009) and *Lusotitan* (P. Mocho, pers. observ., 2011).

The first sacral centrum is strongly convex cranially. The state of the other sacral centra is unknown because they are fused. Excluding the first sacral vertebra, it is possible to recognize, at the dorsocranial area of the lateral face, the presence of transverse processes that are broken at their bases. These transverse processes project craniolaterally and have subrectangular to elliptical cross-sections that are craniocaudally elongated. These structures maintain the same shape and size along the entire sacral sequence.

There is a sequence of three neural spines (two of them fused) that are constricted at their bases (Fig. 11C). The lateral face of these spines presents a smooth subrectangular fossa that is limited by sprl and spol. The triangular dorsal processes of the spines develop toward the lateral face, converging to a pronounced spdl. The spdl is closer to the spol than to the sprl. The dorsal margin of these spines is acute, producing a craniocaudal crest along the dorsal margin of the sacral neural spines. This is considered an autapomorphy of *Lourinhasaurus alenquerensis* (Fig. 11D–F). When the spines are verticalized, the dorsal margin of the sacral spines slopes cranially in lateral view, because the spines become higher caudally (Fig. 11C). Another possibility it is to consider that the dorsal margin of the sacral spines is horizontal, resulting in an important cranial slope of the sacral neural spines, also uncommon in sauropod sacrums (e.g. Osborn, 1904; Osborn & Mook, 1921; Janensch, 1929; Suteethorn *et al*., 2009). Therefore, the marked cranial slope of the dorsal margin of the fused sacral neural spines when verticalized is a unique feature of *Lourinhasaurus alenquerensis*. This configuration could be related to the caudal dorsal deflection of the sacrum. The most caudal sacral spine bears a broad spinopostzygapophyseal fossa (spof) bordered by a thick spol. The cranial and caudal surfaces of this spine are rough, and there is a shallow and wide prespinal process. The dorsal sector of this prespinal process is excavated by a smooth fossa subdivided by a sagittal lamina, considered here as a prespinal lamina (Fig. 11D, E). This configuration is exclusive to *Lourinhasaurus alenquerensis*.

Two fragments of the iliac bar (MG30380) are preserved; they are strongly expanded distally, showing oval outlines in distal view.

Caudal vertebrae: Lapparent & Zbyszewski (1957) recognized five caudal vertebrae. In fact, three proximal caudal vertebrae and two non-corresponding proximal neural spines, as well as several fragments, were identified (Fig. 12). The largest caudal centrum preserves part of its neural arch. The size of the preserved centra compared with that of the sacral centra and the morphology of the neurapophyseal system, which displays an incipient triangular transverse process, suggests that these centra represent proximal caudal vertebrae. By comparison with *Camarasaurus* (Osborn & Mook, 1921) and taking into account the presence of two isolated neural arches (Fig. 12F–K) that are more proximal than the preserved centra (i.e. placed more dorsally and with more pronounced triangular transverse processes), these centra occupy positions between 3 and 8 in the caudal series. The three centra have concave cranial articular surfaces and flat caudal surfaces. The caudal face becomes slightly concave in the centre such as in *Tastavinsaurus* (Royo-Torres, 2009). In general, the centra are craniocaudally short (the ratio between the length and height of the centrum is ≈ 0.58). The centra are slightly transversely constricted at midlength. In cranial and caudal views, the centra are subcircular, narrowing ventrally. Their ventral faces have a slight mediolateral concavity, bordered by smooth crests located at a break of the slope between ventral and medial faces. The lateral faces present neither pleurocoels nor foramina. The transverse processes are laterally projected. The most proximal transverse process found *in situ* (MG4956) bears a distal expansion that is not observed in more caudal isolated available transverse processes (MG30388).

The neural arches are cranially displaced and occupy a large part of the dorsal face of the centrum. The bases of the arches are craniodorsally projected, exceeding the cranial limit of the centrum. In the most proximal caudal centrum, the transverse processes reach the lateral face of the neural arches through a triangular process very similar to the triangular process of *Camarasaurus* (Osborn & Mook, 1921); this process tends to be shallower in more caudal proximal centra. The base of the neural arches is one-third the height of the centrum and encloses a neural canal with a circular cross-section. Distally, the prezygapophyses exceed the level of the cranial articular surface of the centrum. Above and between the prezygapophysis there is an unusually small, circular, deep and well-limited spinoprezygapophyseal fossa (sprf) that is considered an autapomorphy of *Lourinhasaurus alenquerensis* (Fig. 12A, G) but has also been described in *Jobaria* (Sereno *et al*., 1999). The hyposphene ridge, which is slightly fractured, is developed above the neural canal. The prezygapophyses are connected

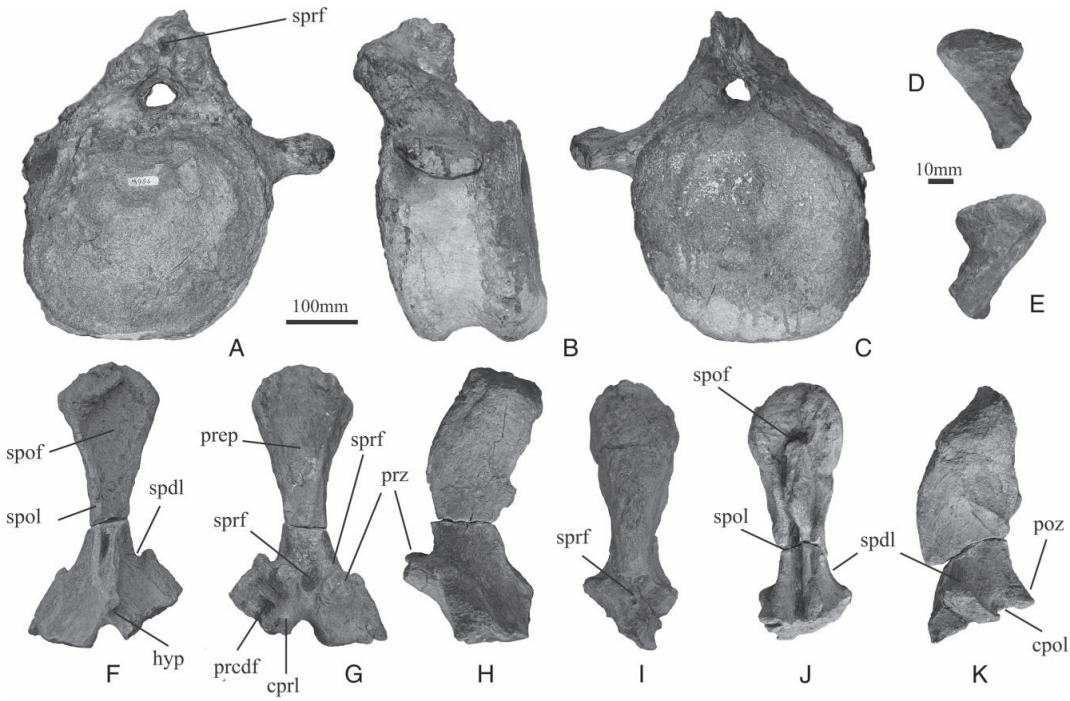

Figure 12. Proximal caudal vertebrae of *L. alenquerensis*. Proximal caudal centra (MG4956) in cranial (A), left (B), and caudal (C) views. Middle chevron articulation of *L. alenquerensis* (MG30387) in caudal (D) and cranial (E) views. Two proximal caudal neural spines (MG30374) in cranial (F and J), caudal (G and I) and left (H and K) views. Traced line: broken borders; fill in traced pinstripes: broken or eroded areas.

to the centrum by a stout structure (cprl) that borders medially the subrectangular prezygapophyseal centrodiapophyseal fossa (prcdf)). This fossa is limited by the lateral margin of the triangular process (probably homologous to the centrodiapophyseal lamina), which emerges dorsally from a knob present in the lateral face of the neural spine.

The most cranial neural spine bears a significant degree of sacralization, suggesting a more cranial position in the series and the possibility that it may be a caudosacral spine (Fig. 12J, K). Nevertheless, it is considered a caudal neural spine because of its overall morphology, the presence of an incipient knob-like process in the lateral face of the base of the neural spine that can be related to other caudal transverse processes with short dorsal bars, and the caudal deflection of the dorsal spine edge. The presence of dorsal bars in the two isolated neural spines suggests the existence of a marked triangular transverse process, at least up to the two first caudal vertebrae.

These two neural spines are robust; the ratio of the height of the most complete neural spine to that of the preserved proximal caudal centra is less than 2. The distal parts of the spines are more expanded transversely than craniocaudally. In cranial view, the most proximal neural spine shows a rounded dorsal margin, while the other has a fan-shaped dorsal margin. The dorsal surface of the most proximal caudal spine slopes cranially, transiting continuously to the cranial face of the spine, and its caudal edge produces a transverse hook-like process in lateral view (Fig. 12K). This feature is not observed in the other preserved spine, which exhibits a straight dorsal edge in lateral view; thus, it is considered a possible autapomorphy. The neural spines display deep spinopostzygapophyseal fossae (spof) that occupy their entire caudal faces. The fossa is bordered by two thick and deep spinopostzygapophyseal laminae (spol) that expand ventrally, giving place to the postzygapophyses, which are not well preserved. The cranial faces of both spines are marked by wide prespinal processes with rough and striated surfaces. These prespinal processes are bordered by grooves and crests that are reminiscent of the sprl.

The most cranial spine shows a more complex structure in the dorsal sector of its transverse process; a smooth spinodiapophyseal lamina (spdl) and a probable prezygodiapophyseal lamima (prdl) emerge from the dorsal bar. These laminae limit a small and smooth spinodiapophyseal fossa (sdf). Between the spdl and the spol there is a smooth fossa, a subtriangular to subrectangular postzygapophyseal spinodiapophyseal fossa (posdf) that disappears toward the dorsal area. This fossa is bordered ventrally by a marked, arched, short centropostzygapophyseal lamina (cpol) that in lateral view marks a circular recess that is not present on the left side. Medially to this lamina, a small circular fossa is present.

Chevrons: Only a few distal and proximal fragments of chevron were identified in the sample (Fig. 12D, E). It is possible to recognize the absence of a bridge connecting the proximal ends, at least, in the middle chevrons. The proximal facet has an elliptical outline with a medial process.

Appendicular skeleton

Left and right scapulae: The complete left scapula and the proximal part of the right scapula are preserved (Fig. 13A, D, E). This element is laterally convex and has a significant expanded acromion process that is twice the maximum height of the scapular blade. This process is thicker at its ventral edge (in the glenoid) and becomes thinner craniodorsally. In lateral view, the acromion process has a semicircular to subrectangular outline with a straight caudodorsal edge. The acromial ridge close to the acromion caudal margin has a dorsoventral orientation and deflects cranioventrally, becoming less pronounced towards the ventral margin. Caudal to the acromial ridge, the surface of the acromion process is concave. The scapular fossa has a dorsoventral elliptical outline

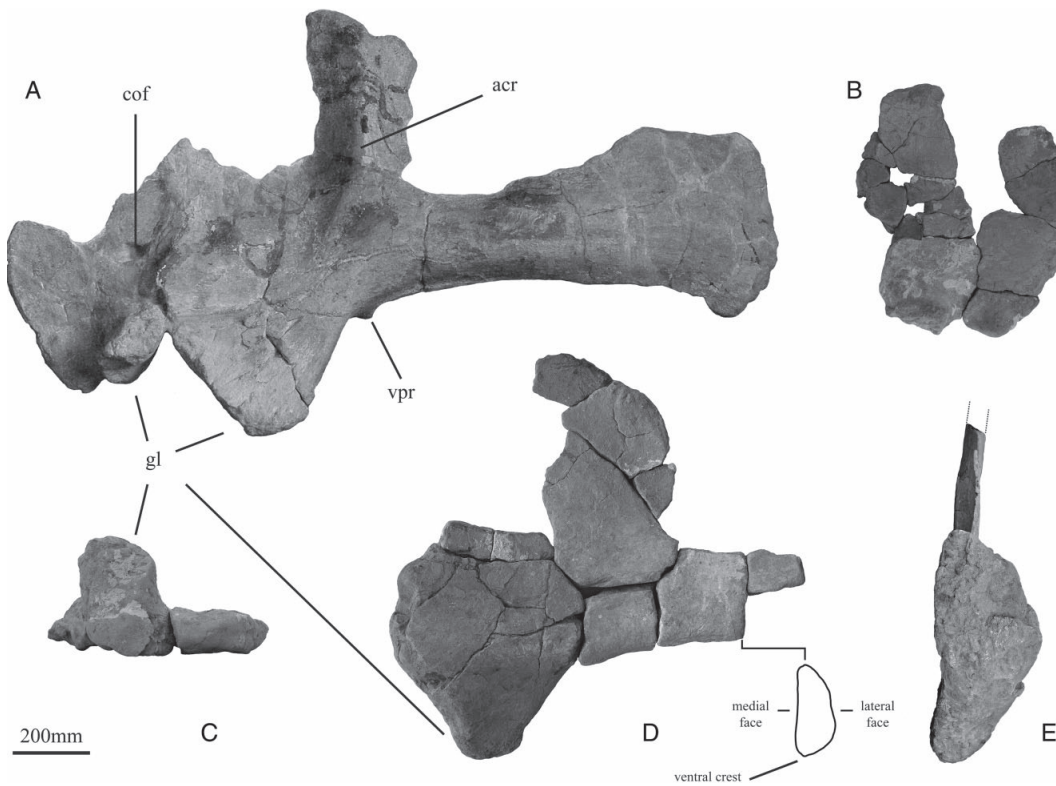

Figure 13. Scapular girdle of *L. alenquerensis*. Left scapula and coracoid (MG5780) in lateral view, right scapula (MG30371) in medial (D, black line: cross section of scapular blade) and proximal (E) views and right coracoid (MG 30372) in lateral (B) and ventral (C) views.

and occupies nearly two-thirds of the acromion process. The proximal surface, facing cranially, is rough and bears a lenticular to 'D'-shaped cross-section with a straight lateral edge (Fig. 13E). Above the glenoid, it is possible to identify a concavity in the proximal surface that corresponds to the indentation between the scapula and the coracoids. The glenoid faces ventrally. In the ventral margin of the scapular blade, near the acromion process, there is a protuberance (Fig. 13A, D) from which a rough crest departs, giving a slightly acute profile to the ventral margin. The lateral side of this crest is bordered by a groove. The scapular blade is expanded distally. This expansion is subquadrangular and bears a distoventral hook-like protuberance. Its distal surface is rough. The scapular blade is thicker near its ventral edge, resulting in a D-shaped cross-section. The lateral face of the scapular blade is slightly convex craniocaudally and strongly convex dorsoventrally, and the medial surface is flat to concave.

Left and right coracoids: The left and the right coracoids were found in anatomical connection with their respective scapulae (Fig. 13A–C). Currently it is not possible to reconstruct the dorsal margin of any of them, but they had a subquadrangular outline, as can be interpreted from the photographic record of the *Lourinhasaurus* excavation (Lapparent & Zbyszewski, 1957: plate VI, fig. 2). The cranial edge of both coracoids is convex in lateral view and the dorsal margin of coracoids does not surpass the dorsal margin of the scapula. The coracoids are dorsolaterally elongated and thicker at the glenoid sector, producing a concave surface on both sides of the coracoids. The glenoid is thick and laterally projected (Fig. 13C) bearing a rough, flat and sigmoid facet, facing ventrally. Cranial to the glenoid, there is a circular recess of the coracoid ventral margin. Between the glenoid and the coracoidal foramen, the caudal margin bears a concavity corresponding to the attachment area for the scapula. The coracoidal foramen is elliptical, elongated craniocaudally and with a caudomedial development.

Sternal plates: In the sample are two sternal plates (Fig. 14) not referred to by Lapparent & Zbyszewski (1957). These two elements have a similar mediolateral width and probably correspond to the right and left sternal plates. The left one could correspond to a cranial sector of the sternal plate and the right one to the caudal sector. With both fragments it is possible to infer a craniocaudally elongated oval outline for the complete sternal plate. In ventral view, the medial margin is convex and the lateral margin is straight to slightly concave. In the medial edge of the right sternal plate (MG30382) it is possible to observe the zone of articulation between both sternal plates.

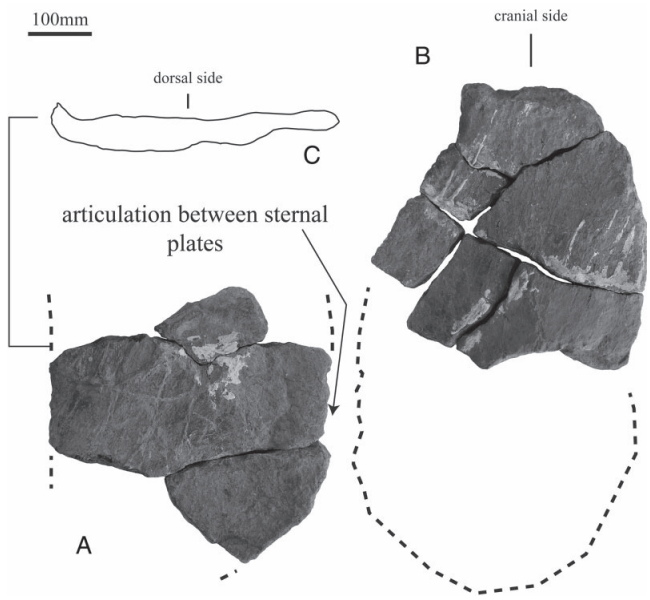

Figure 14. Sternal plates of *L. alenquerensis*. Right (MG30382) (A) and left (MG30383) (B) sternal plates in ventral view and the cross-section of the right one (C). The traced line indicates lost bone.

The region for the attachment of sternal ribs is not preserved. The sternal plates become thicker near the lateral and cranial margin. These plate-like elements are dorsally concave and ventrally convex. The axis of this convexity is close to the lateral margin. In the surface of these bones there is a particular bone texture formed by cross-linked fibres. The margins of these plates are rough. Cranially it is possible to identify a triangular phalanx-like process.

Left and right humeri: The humerus is slightly curved, with a convexity caudal and laterally directed (Fig. 15A–E). The diaphysis has an elliptical cross-section, craniocaudally compressed. The proximal section is strongly expanded mediolaterally with proximal, lateral, and medial margins cranially projected producing a wide and deep teardrop-shaped depression. The cranial face of the proximal section bears a small circular depression near the proximal margin. The humeral head is proximomedially projected. The proximolateral corner is rounded. A deltopectoral crest runs along the lateral edge of the humerus from the proximal margin up to its midlength. This crest is craniolaterally projected and its transverse outline is subrectangular. The proximal surface is rough and the humeral head occupies two-thirds of this surface (with an oval to elliptical proximal outline). The distal portion of the left humerus is well preserved (but covered with plaster) and some fragments of the right humerus distal section were also identified. The distal section has a slight mediolateral expansion (corresponding to two-thirds of the proximal portion of the mediolateral expansion). The cranial and caudal faces of the distal region are flat and flat-to-concave, respectively. The craniolateral sector of the distal region bears two rough protuberances. The distal surface is flat and rough and the ulnar and radial condyles are not separated by a marked intercondylar groove. The radial condyle is more expanded and polygonal than the ulnar condyle. The humerus/femur length ratio is 0.82.

Left radius: The radius (Fig. 16A–E) is cylindrical and arched longitudinally with its convexity cranially orientated. The proximal portion is expanded in a craniomedial-to-caudolateral direction, and its cranial margin exhibits an acute profile. Parting from the cranial edge of the proximal surface is a crest that disappears distally and is replaced by another more medial crest. The latter crest ends in a triangular facet. In proximal view, the outline of the proximal surface is elliptical, with a concave and rough

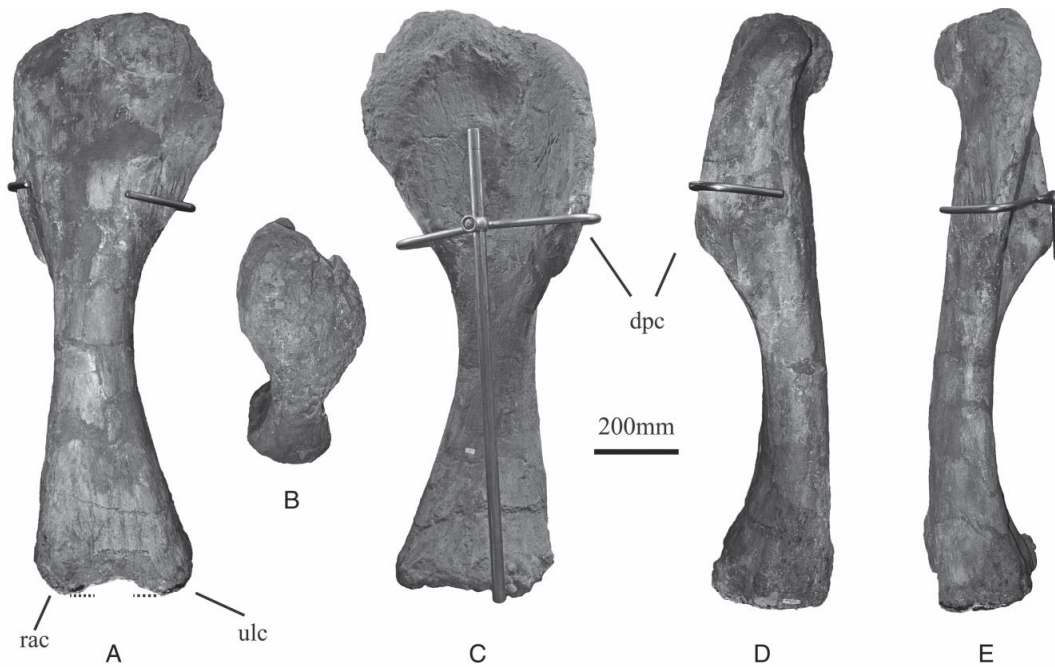

Figure 15. Forelimb of *L. alenquerensis*. Left humerus (MG2) in caudal (A), cranial (B), lateral (C), medial (D), and proximal (E) views. The traced line indicates lost bone.

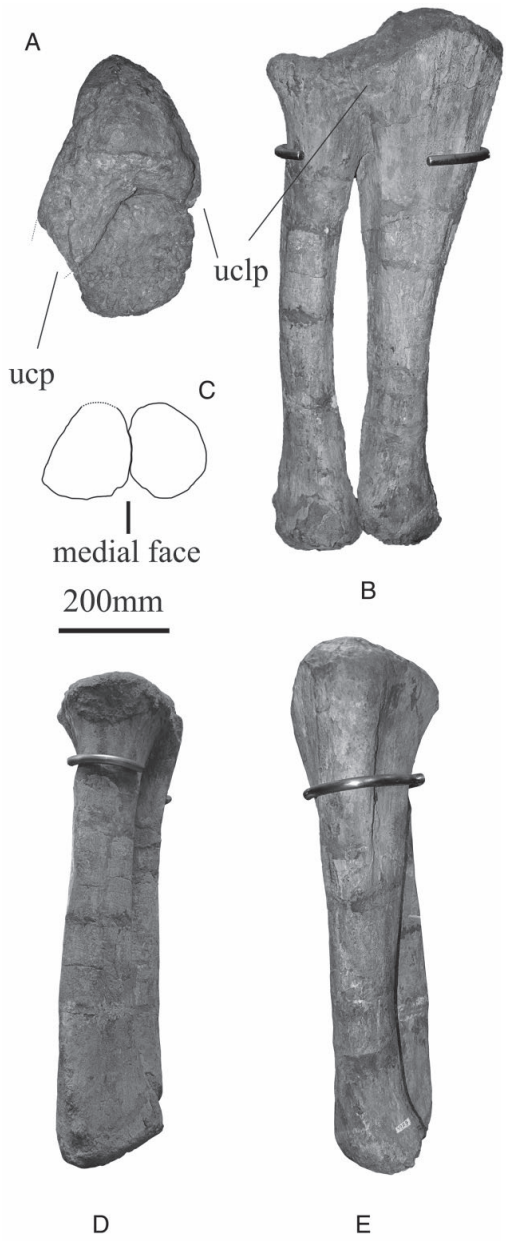

Figure 16. Left radius and ulna (MG4979) in proximal (A), lateral (B), cranial (D), caudal (E) views, and the outline of the distal view (C). Traced line: broken borders.

surface (Fig. 16A). The diaphysis is compressed craniolaterally to caudomedially. In the caudal face, from the diaphysis towards the distal portion, there is a proximodistal groove bordered by two crests. In distal view, this groove has a semicircular outline with a straight cranial margin; it has a rough and convex surface.

Left ulna: The left ulna is preserved and is associated with the left radius (Fig. 16A–E). In proximal view, the ulna has a triradiate outline (Fig. 16A) composed of three vertices: (1) a craniolateral process (distal sector slightly damaged), (2) a cranial process (distally damaged), and (3) a rounded caudal apex. Although partially broken, the cranial process is longer and more robust than the craniolateral process. This triradiate outline extends to the midlength of the ulna. The proximal surface is convex with its highest point located on its centre. The surfaces of the cranial and craniolateral processes are flat and present straight profiles in medial and caudolateral views. The ulnar shaft has an oval-to-circular transverse section. On the cranial face of the ulnar shaft, there is a proximodistal crest that extends distally to the vertex of a triangular facet, the distal portion of which projects slightly toward the medial side. The distal surface of the ulna is rough and convex with an oval outline elongated mediolaterally and has an acute margin on the craniomedial side.

Carpal II: The carpus is poorly known in sauropods (Upchurch *et al*., 2004) and the interpretation was based in some previous occurrences (e.g. Osborn, 1904; Ostrom & McIntosh, 1966; Bonnan, 2003; Royo-Torres *et al*., 2006; R. Royo-Torres, pers. observ., 2013). The element MG30385 is considered as carpal II (Fig. 17). Lapparent & Zbyszewski (1957) noted the existence of a carpal II in *Lourinhasaurus*, but it was never described before and probably corresponds to the same bone. This element is block-shaped, with a flat proximal surface which could be interpreted as the area for reception of the distal portion of the ulna and a concave distal surface. The putative distal surface, with a D-shaped outline in proximal view, bears a central circular process that could be considered an autapomorphy of *Lourinhasaurus alenquerensis* (Fig. 17D, E).

Left ilium: The outline of the iliac blade is semicircular (Fig. 18). The lateral face of the ilium cannot be described because is in exhibition and covered by a plaster platform. The iliac blade is vertical with a slight medial slope and has a convex dorsal margin that becomes straight toward the postacetabular process. The preacetabular process is thick, craniolaterally orientated and has a subtriangular

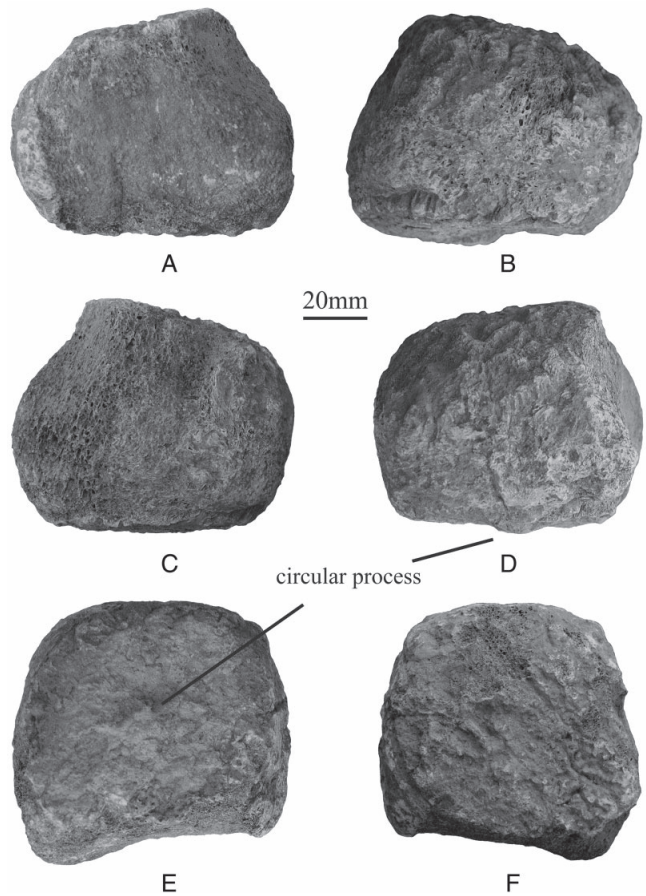

Figure 17. Carpal II of *L. alenquerensis* (MG30385) in medial? (A), lateral? (B), cranial? (C), caudal? (D), distal (E), and proximal (F) views.

outline in medial view. The postacetabular process is caudally orientated, and the chord through the ischiatic and pubic articulations passes through the ventral margin of the postacetabular process. This combination is considered an autapomorphy of *Lourinhasaurus alenquerensis*. The medial surface of the ilium, corresponding to the area of attachment of the sacral ribs, has a few dorsoventral crests that reach the dorsal margin of the iliac blade. In the ventral margin of the postacetabular process there is a rough and oval craniocaudal crest, a feature that is considered an autapomorphy of *Lourinhasaurus alenquerensis* (Fig. 18B). A strong pubic peduncle is laterally expanded and subrectangular in cranial view with a convex-to-acute cranial surface. The caudal surface of this peduncle is markedly concave, and the outline of its distal surface is semicircular to teardrop-shaped. The ischiatic peduncle is weakly developed and laterally orientated. In the base of the pubic peduncle, an oval protuberance is observed.

Left and right pubis: The two pubis of the type individual were recovered (Fig. 19). The iliac peduncle is dorsally projected and radially expanded with a rough and flat surface and a heart-shaped to elliptical outline in proximal view (Fig. 19C). The semicircular acetabulum is an individualized and well-marked surface that is distinguishable from the iliac and ischiatic peduncles. The obturator foramen is closed and has an elliptical outline that is craniocaudally elongated. The pubic blade lies in the same plane as the proximal plate and has a teardrop-shaped cross-section. The pubic blade has the same orientation as the ischiatic peduncle (i.e. they are parallel), a feature

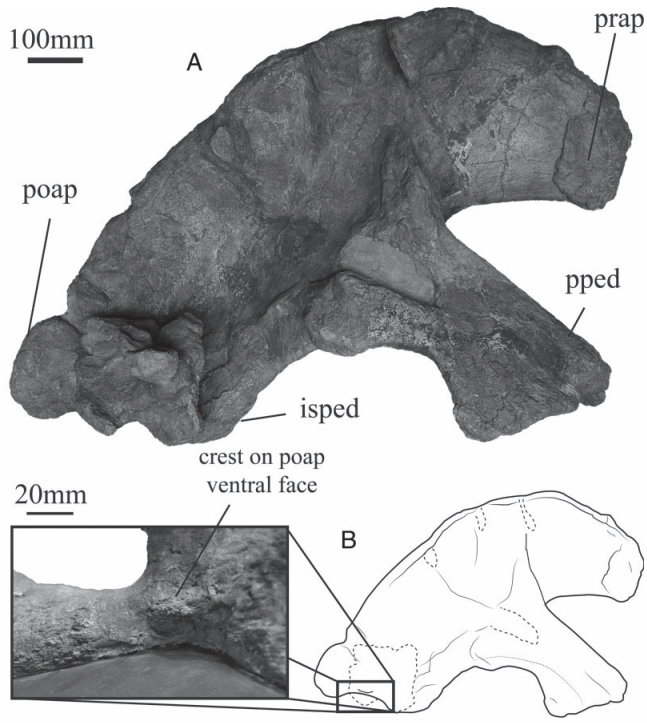

Figure 18. Left ilium of *L. alenquerensis* (MG5781) in medial view (A). The base of postacetabular process (poap) in ventral view (left) noted in a schematic figuration of the ilium (right) (B). Traced line: broken borders or superimposing bone.

that is considered an autapomorphy of this taxon (Fig. 19A). In caudal view below the ischiatic peduncle, the pubic blade becomes thinner and deflects medially, producing a caudal margin with an s-shaped profile (Fig. 19B). The cranial edge of the iliac peduncle is flat and bears a triangular striated facet. The distal part of the pubis is expanded, forming an oval, rough, convex tip. The distal part of the pubic blade has a mediocranial expansion and displays a hook-shaped profile in lateral view resulting from the dorsal projection of the cranial tip.

Left and right ischia: The two ischia are preserved but slightly fractured in the ventral margin of the proximal plate (Fig. 20). The iliac peduncle is oval, is compressed mediolaterally (more pronounced on the right ischium), and has a convex and rough surface. The pubic peduncle has an arched profile in lateral view; in cranial view it presents a rough surface with a subrectangular outline where its width decreases ventrally. This surface has, at midlength, a lip-like structure on its lateral edge. The two peduncles are separated by a deep and well-differentiated acetabulum. The lateral edges of this surface are uplifted, producing a crest that is caudally flanked by a marked groove. The presence of this crest is considered an autapomorphy of *Lourinhasaurus alenquerensis* (Fig. 20C, E). The ischiatic blade twists nears its distal end and the ischiatic blades become almost co-planar. The distal symphysis is short and has a teardrop outline. Near the pubic peduncle, the ventral margin of the ischiatic proximal plate has a v-shaped symphysis. The cross-section of the ischiatic blade has a teardrop outline with an acute ventral edge (the ventral margin bears a longitudinal crest). The angle between the ischiatic blade and the pubic peduncle is approximately 80° (the long axis of the blade passes through the pubic peduncle). On its lateral face near its dorsal margin and close to the proximal plate, the ischiatic blade bears a small tuberculum (50 mm) bordered by a parallel groove. The medial face of the ischiatic blade also bears a proximodistal crest that runs through it from its dorsal (proximal) to its ventral (distal) edge. The

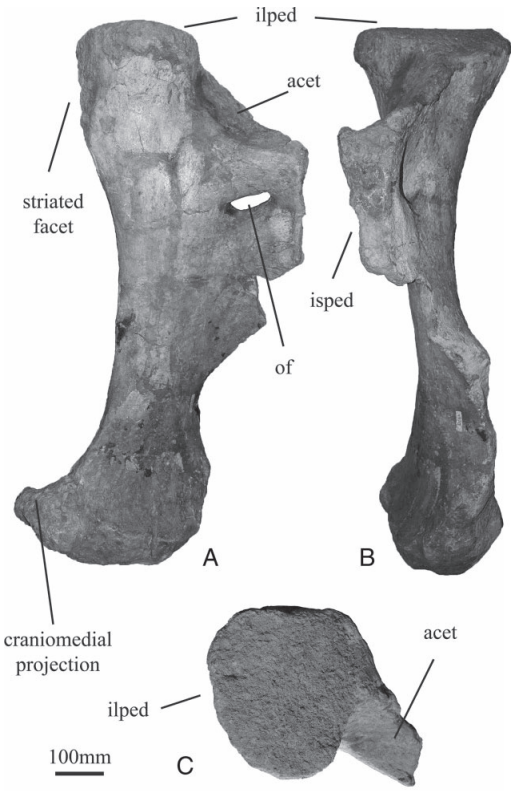

Figure 19. Left pubis of *L. alenquerensis* (MG 4970) in lateral (A), caudal (B), and proximal (C) views.

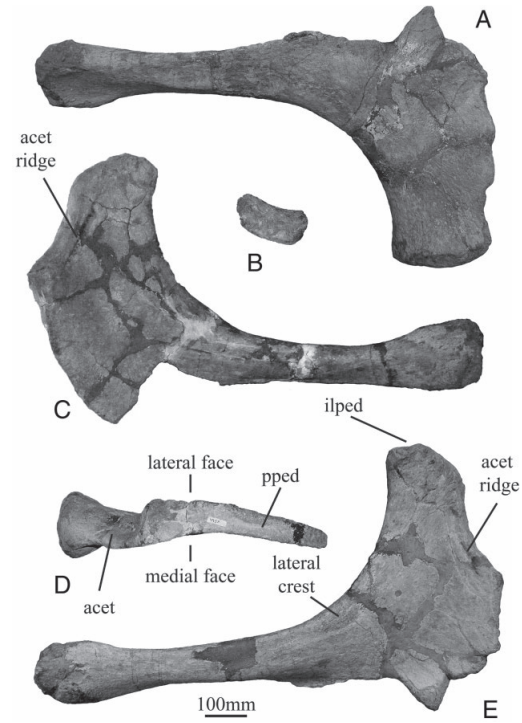

Figure 20. Ischia of *L. alenquerensis* (MG4957). Left ischium in distal (B), lateral (C) and cranial (D) views, and right ischium in medial (A) and lateral (E) views.

distal part of the ischium is slightly expanded; in distal view, it shows a subrectangular arched outline with a concavity facing dorsally. The distal surface is flat and rough (Fig. 20B).

Left femur: The femur is straight and craniocaudally compressed, resulting in an elliptical cross-section (craniocaudal/mediolateral length ratio: 0.58). The femoral shaft shows a marked medial deflection without a lateral bulge (Fig. 21A, B), a unique combination in sauropods (see explanation in fibula description). In the femur of *Lourinhasaurus*, the diaphysis makes an angle of approximately 10° with the vertical axis when the distal condyles are situated in the horizontal plane (Fig. 21B). Proximally, on the lateral face of the femur, there is a shallow crest at the location of the lesser trochanter. The femoral head, being medially wide, is slightly proximomedially projected. The 4th trochanter is elongated proximodistally and located at the medial edge of the femoral caudal face. Its distal tip is situated at midshaft. The 4th trochanter is bordered laterally by a proximodistal elliptical concavity and medially by a wide and smooth concavity. The proximal surface of the femur is rough and is lacking part of the femoral head cranial edge (Fig. 21C). The distal part of the femur becomes larger medially and laterally, bearing the tibial and the fibular condyles with convex and rough proximal surfaces. The tibial condyle is caudally projected; in caudal view, it presents a subtriangular outline that is lateromedially compressed. The distal outline of the fibular condyle is more polygonal than the outline of the elliptical tibial condyle (Fig. 21D). On the caudal surface of the tibial distal section, there is a deep intercondylar groove that continues to the caudal surface. The cranial face of the distal section is smoothly concave, and the condyles are not present in this region.

Left tibia: The tibial diaphysis is straight and has an elliptical to subcircular cross-section (craniolaterally to caudomedially elongated) (Fig. 22A–D). The proximal portion, which has a slightly fractured lateral

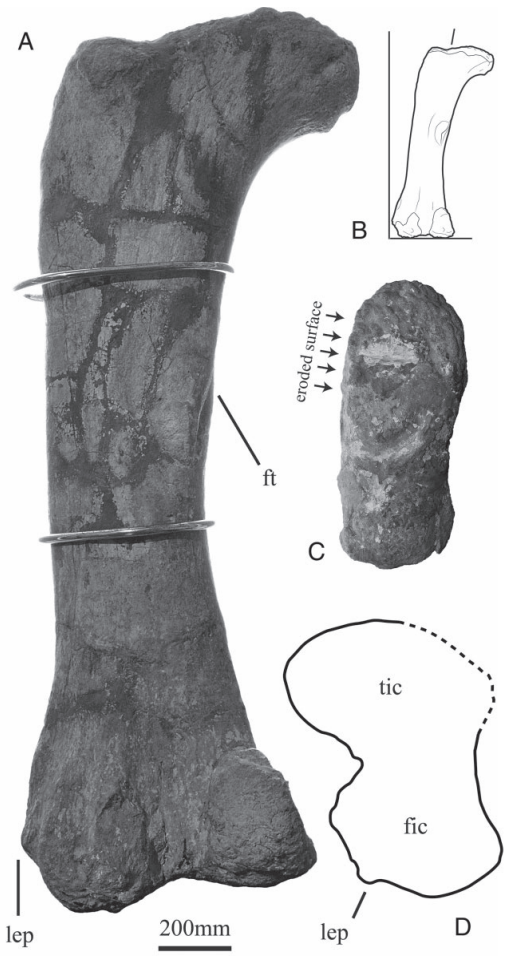

Figure 21. Left femur of *L. alenquerensis* (MG4931) in caudal (A) and proximal (C) views, and the outline of distal view (D). Outline of *L. alenquerensis* femur without scale, showing the marked medial deflection of the femur shaft when the tibial and fibular condyles are in the horizontal plane (B). Traced line: broken borders.

edge, is expanded, and the craniocaudal diameter of the proximal end is only 8% greater than its transverse diameter (Fig. 22C). The proximal surface is rough and flat to concave. At the cranial margin of the proximal section stands the subtriangular cnemial crest, which is laterally projected (the vertex of this crest also has a lateral orientation). The fibular articulation is well defined and bears a rough surface. It is separated from the cnemial crest by a proximodistal groove. The preservation of the lateral margin of the proximal section (the proximal sector of the fibular articulation) does not permit testing for the presence of a projected edge ('second cnemial crest' *sensu* Bonaparte, Heinrich & Wild, 2000), a feature that is present in other sauropods (Mannion *et al*., 2013). The expansion of the distal section is less pronounced than the proximal expansion and, in distal view, it is subrectangular and slightly compressed transversally. The posteroventral process is suboval, craniocaudally elongated and separated from the articular surface for the ascending process by a groove with a subcircular outline (Fig. 22D). This groove is evident on the caudal face of the distal section. The distal surface of the posteroventral process and the articular surface for the ascending process tibia are rough and convex. The ratio between tibia and femur lengths is 0.65.

Left fibula: The fibula has a general incipient sigmoid form; it is almost straight, with expanded proximal and distal ends (Fig. 22E–J). In cranial view (Fig. 22G), the fibula shows a generally straight profile with a slight laterocaudal deflection of its proximal portion at the level of the lateral trochanter. The lateral trochanter presents a proximodistal development and a sigmoid shape, with its distal tip directed toward the shaft caudal margin. In lateral view, the proximal and distal edges are straight and semicircular, respectively (Fig. 22I, J). The anterior trochanter is placed at the proximal third of the fibula. It is rounded and proximodistally elongated; it is craniomedially directed and does not produce a crest-like structure. The proximal sector of this trochanter is absent. The medial face of the proximal section is flat and somewhat eroded. Despite this erosion, it is possible to recognize the limits of the triangular tibial articular surface with its distal tip above the apex of the anterior trochanter (Fig. 22H). In cross-section, the fibular shaft is elliptical (elongated craniocaudally). In proximal view (Fig. 22E), the fibula is subrectangular (fractured cranially) and slightly arched, with its convexity orientated laterally. The distal surface is convex and has a transverse semicircular outline (Fig. 22F). The medial face of the distal section is medially projected and bears a proximodistal groove. The tibia and the fibula are of equal length, implying a more distal position of the fibula relative to the tibia for the reception of the astragalus, a feature considered an autapomorphy of *Lourinhasaurus alenquerensis*. In sauropods, the fibula is generally taller than the tibia because it has an area for the reception of the lateral face of the astragalus. Nevertheless, in *Lourinhasaurus alenquerensis*, the tibia and fibula are similar in height and when the proximal sections of both elements are at the same level, the astragalar

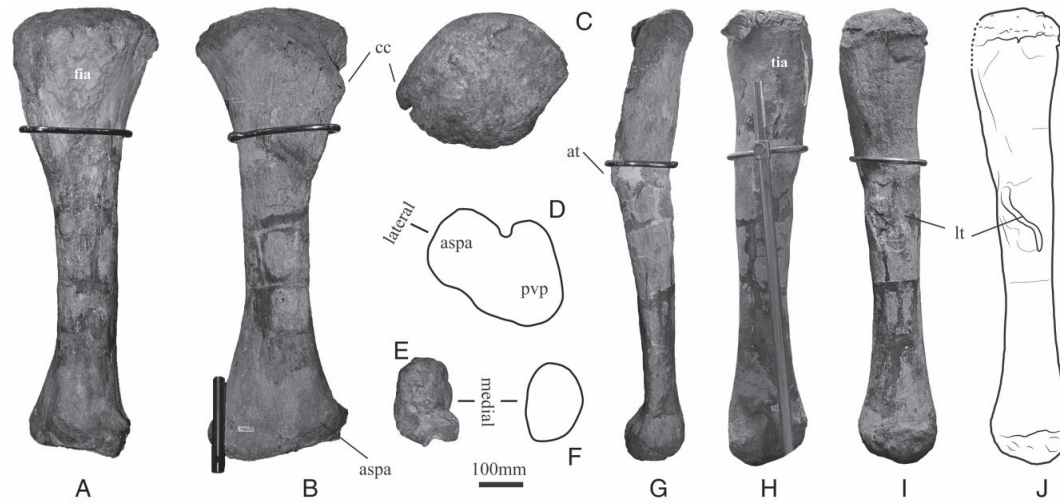

Figure 22. Left tibia (MG4983) and fibula (MG4984) of *L. alenquerensis.* Tibia in lateral (A), cranial (B), and proximal (C) views, and the outline of distal view (D). Fibula in proximal (E), cranial (G), medial (H), and lateral (I) views, schematic interpretation of lateral view (J) and the outline of its distal view (F). Traced line: broken borders.

articular face of the fibula are at the same level as the tibial distal section, and cannot articulate with the astragalus. This could be related to the medial deflection of the femur shaft described above. If the femur shaft is in vertical position, the fibular condyle occupies a more distal position than the tibial condyle, resulting in a more distal position of the fibula relative to the tibia. With a more distal position of the fibula, the astragalar articulation face could articulate with the lateral face of the astragalus.

Left astragalus: The available astragalus is a robust element, fragmented at its medial edge (Fig. 23). The distal face is rough and transversally convex (Fig. 23C). In cranial view, it has a wedge-shaped format (higher at the lateral edge). By contrast, in lateral view, the astragalus bears a semicircular outline and has subcircular concavity (= fibula articular surface) (Fig. 23B). The posterior astragalar fossa slopes caudally. In this fossa there is a deep and circular foramen (Fig. 23D) that pierces the concave caudal surface of the ascending process. The ascending process of the astragalus is broken caudally, and it is thus impossible to interpret if this process reaches the caudal edge of thge astragalus. In distal view, just behind the caudomedial edge of the ascending process, the caudal margin becomes slightly acute. Parting from the caudomedial corner of the ascending process is a crest that borders medially the circular foramen referred to above and subdivides the posterior astragalar fossa.

Right pedal (?) phalanx II: Besides the reference to a manual phalanx found from Moinho do Carmo quarry (Lapparent & Zbyszewski, 1957), we considered this phalanx more similar to pedal phalanges, probably a pedal phalanx II (Fig. 24). This phalanx (ventral face strongly damaged) has a proximodistal/mediolateral width ratio close to 1. Along its proximodistal length the phalanx are lateromedially constricted. The lateral edge is shorter proximodistally than the medial edge. The proximal surface is slightly concave, smooth and with some grooves. In proximal view, the dorsal edge of this surface bears a concavity that has small expression in the proximal sector of the phalanx dorsal surface. The distal surface is probably convex, but the preservation does not allow describing it in detail.

PHYLOGENETIC ANALYSIS

Analyses

To provide a phylogenetic analysis for *Lourinhasaurus alenquerensis* we used the data matrices proposed by Wilson (2002) and Upchurch *et al*. (2004) including some modifications and updates subsequently proposed by several authors, such as: (1) recodification of *Euhelopus* proposed by Wilson & Upchurch (2009); (2) integration of *Tastavinsaurus* codified by Royo-Torres *et al*. (2012) from two specimens; (3) introduction of the Spanish Upper Jurassic taxa *Galveosaurus*, *Losillasaurus*, and *Turiasaurus* (Royo-Torres *et al*., 2006; Royo-Torres & Upchurch, 2012).

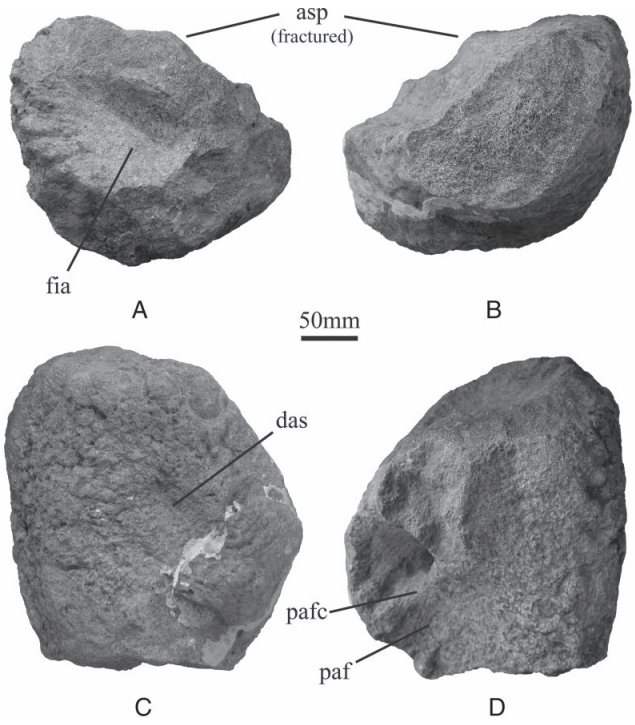

Figure 23. Left astragalus of *L. alenquerensis* (MG30375) in medial (A), lateral (B), ventral (C), and dorsal (D) views.

For the Wilson (2002) data matrix we introduced several modifications, some of them already proposed by Royo-Torres & Upchurch (2012) and Royo-Torres *et al*. (2012): (1) incorporation of *Phuwiangosaurus* (based on Suteethorn *et al*., 2010), *Cedarosaurus* and *Venenosaurus* (both based on Tidwell, Carpenter & Brooks, 1999; Tidwell, Carpenter & Meyer, 2001; Canudo, Royo-Torres & Cuenca-Bescós, 2008; D'Emic, 2012, 2013), and *Tehuelchesaurus* (based on Carballido *et al*., 2011); and (2) modifications for *Mamenchisaurus* and *Omeisaurus* obtained from Harris (2006). For the Upchurch *et al*. (2004) data matrix and based on recent publications we applied some modifications in *Tastavinsaurus* (Canudo *et al*., 2008; Royo-Torres *et al*., 2012), *Cedarosaurus* (D'Emic, 2012, 2013), and *Tehuelchesaurus* (Carballido *et al*., 2011). From the *Brachiosaurus* operational taxonomic unit (OTU) of Wilson (2002) and Upchurch *et al*. (2004) data matrix and based on Janensch (1936, 1950, 1961) and Taylor (2009), we replace this OTU by *Giraffatitan*. All new changes proposed in this study are detailed in the supporting information.

Data matrices were analysed using TNT 1.1 (Goloboff, Farris & Nixon, 2003) to find the most parsimonious trees (MPTs). We used a heuristic tree search performing 1000 replications of Wagner trees (using random addition sequences) followed by tree bisection reconnection (TBR) as swapping algorithm, saving 100 trees per replicate. To test the support of the phylogenetic hypotheses, Bremer support and bootstrap (absolute frequencies based on 5000 replicates) values were obtained in TNT 1.1. (Goloboff *et al*., 2003). Some constrained analyses were carried out in TNT, to compare with previous phylogenetic approaches. The resulting MPTs were exported to PAUP 4.10b (Swofford, 2002) to run Templeton's tests of the unconstrained and constrained topologies.

RESULTS

The revision of the lectotype of *Lourinhasaurus alenquerensis* provides a revised codification for the Upchurch *et al*. (2004) data matrix and a codification for the Wilson (2002) data matrix. The results always place *Lourinhasaurus* as a basal macronarian (*sensu* Wilson & Sereno, 1998), supporting the hypotheses of Royo-Torres *et al*. (2006) and Barco (2010), and as a basal member of the Camarasauromorpha clade. However, note that the bootstrap support values

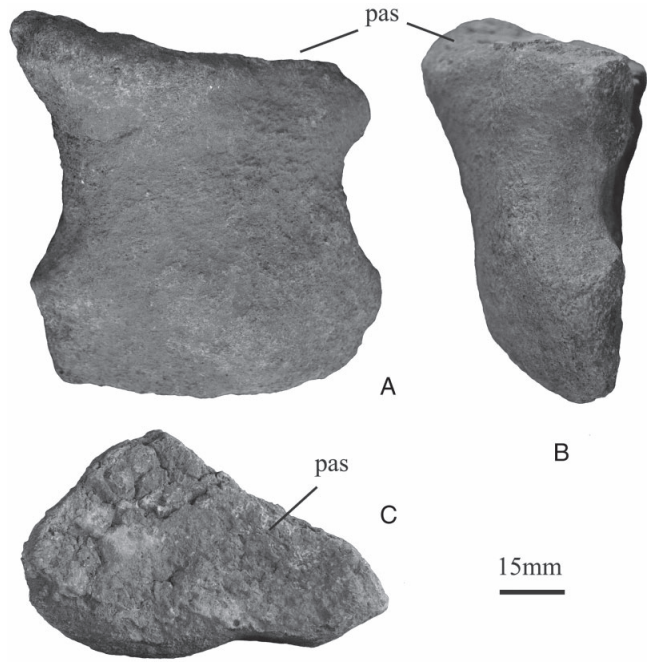

Figure 24. Right pedal (?) phalange II of *L. alenquerensis* (MG30386) in dorsal (A), lateral (B), and proximal (C) views.

for the Macronaria and Camarasauromorpha node based on Upchurch *et al*.'s (2004) and Wilson's (2002) data matrices are generally low (see supporting information).

Analysis I, based on Wilson's (2002) data matrix

As in the original analysis (Wilson, 2002), the multistate characters 8, 37, 64, 66, and 198 were considered ordered. The result of this analysis yielded ten MPTs of 519 steps with a consistency index (CI) of 0.551 and a retention index (RI) of 0.739 (Fig. 25A). The general topology obtained is similar to that proposed by Royo-Torres & Upchurch (2012), resembling the general of topology yielded by the previous Wilson (2002) hypothesis. In this phylogenetic hypothesis *Jobaria* is placed in a polytomy with Neosauropoda. Moreover, Royo-Torres *et al*. (2012) obtained a more derived position for Laurasiformes (*Cedarosaurus*, *Tastavinsaurus*, and *Venenosaurus*) including them inside Somphospondyli. In this phylogenetic hypothesis Laurasiformes is also recovered as a monophyletic clade inside Somphospondyli but in polytomy with *Euhelopus* and *Phuwiangosaurus*.

The results obtained propose *Lourinhasaurus* as a member of Macronaria (*sensu* Wilson & Sereno, 1998) by the presence of opisthocoelous caudal dorsal centra (character 105) and cranial dorsal ribs with plank-like cross-section (character 142). In this analysis, Camarasauridae *sensu* Taylor & Naish (2007) is recovered as a monophyletic clade, comprising *Tehuelchesaurus*, *Camarasaurus*, and *Lourinhasaurus*, being supported by the absence of a pcpl in the middle and posterior vertebrae (character 98) and the transverse width of the proximal caudal neural spines being greater than 50% of its craniocaudal width (character 126).

Tehuelchesaurus is recovered as a camarasaurid in the proposed phylogenetic analyses; nevertheless, several authors consider it as more derived than *Camarasaurus* (Carballido *et al*., 2011; D'Emic, 2012; Carballido & Sander, 2013). Carrying out an analysis in which *Tehuelchesaurus* is removed a priori yielded six MPTs with 511 steps and CI = 0.560 and RI = 0.748. Camarasauridae (*Lourinhasaurus*+ *Camarasaurus*) is also recovered with improved Bremer support (2).

Analysis II, based on Upchurch *et al*.'s (2004) data matrix

As in the original analysis (Upchurch *et al*., 2004), *Marasuchus* is considered as an outgroup the following taxa are omitted a priori: *Aragosaurus*,

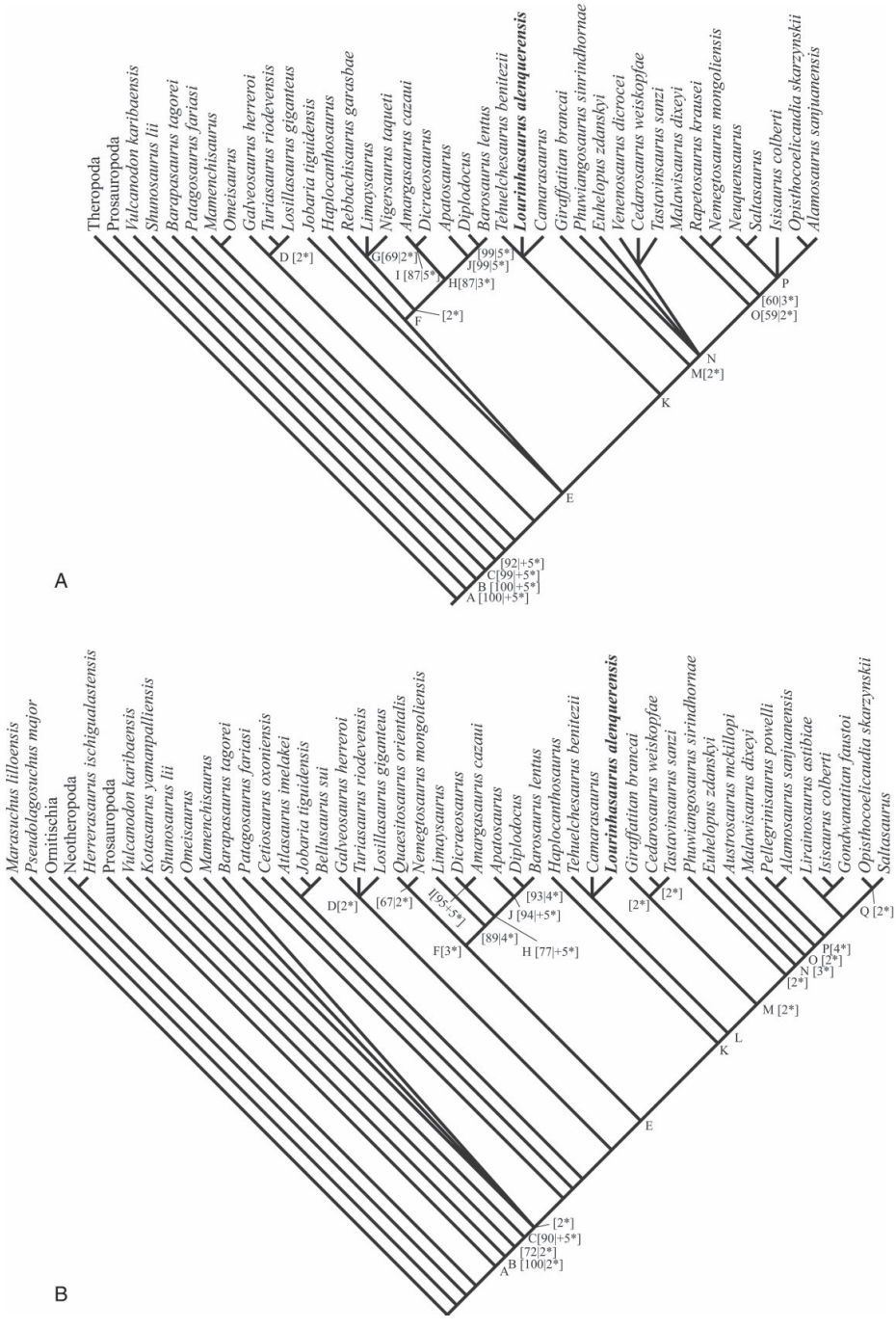
A
Theropoda
Prosauropoda
Vulcanodon karibaensis
Shunosaurus lii
Barapasaurus tagorei
Patagosaurus fariasi
Mamenchisaurus
Omeisaurus
Galveosaurus herreroi
Turiasaurus riodevensis
Losillasaurus giganteus
Jobaria tiguidensis
Haplocanthosaurus
Rebbachisaurus garasbae
Limaysaurus
Nigersaurus taqueti
Amargasaurus cazaui
Dicraeosaurus
Apatosaurus
Diplodocus
Barosaurus lentus
Tehuelchesaurus benitezii
Lourinhasaurus alenquerensis
Camarasaurus
Giraffatitan brancai
Phuwiangosaurus sirindhornae
Euhelopus zdanskyi
Venenosaurus dicrocei
Cedarosaurus weiskopfae
Tastavinsaurus sanzi
Malawisaurus dixeyi
Rapetosaurus krausei
Nemegtosaurus mongoliensis
Neuquensaurus
Saltasaurus
Isisaurus colberti
Opisthocoelicaudia skarzynskii
Alamosaurus sanjuanensis
D [2*]
G[69|2*]
I [87|5*]
J[99|5*]
H[87|3*]
F
[2*]
[99|5*]
P
[60|3*]
O[59|2*]
N
M[2*]
K
E
[92|+5*]
C[99|+5*]
B [100|+5*]
A [100|+5*]
B
Marasuchus lilloensis
Pseudolagosuchus major
Ornithischia
Neotheropoda
Herrerasaurus ischigualastensis
Prosauropoda
Vulcanodon karibaensis
Kotasaurus yamanpalliensis
Shunosaurus lii
Omeisaurus
Mamenchisaurus
Barapasaurus tagorei
Patagosaurus fariasi
Cetiosaurus oxoniensis
Atlasaurus imelakei
Jobaria tiguidensis
Bellusaurus sui
Galveosaurus herreroi
Turiasaurus riodevensis
Losillasaurus giganteus
Quaesitosaurus orientalis
Nemegtosaurus mongoliensis
Limaysaurus
Dicraeosaurus
Amargasaurus cazaui
Apatosaurus
Diplodocus
Barosaurus lentus
Haplocanthosaurus
Tehuelchesaurus benitezii
Camarasaurus
Lourinhasaurus alenquerensis
Giraffatitan brancai
Cedarosaurus weiskopfae
Tastavinsaurus sanzi
Phuwiangosaurus sirindhornae
Euhelopus zdanskyi
Austrosaurus mckillopi
Malawisaurus dixeyi
Pellegrinisaurus powelli
Alamosaurus sanjuanensis
Lirainosaurus astibiae
Isisaurus colberti
Gondwanatitan faustoi
Opisthocoelicaudia skarzynskii
Saltasaurus
D[2*]
[67|2*]
[93|4*]
J [94|+5*]
[89|4*]
F[3*]
H [77|+5*]
[2*]
[2*]
Q [2*]
P[4*]
O [2*]
N [3*]
[2*]
M [2*]
K
L
E
[2*]
C[90|+5*]
[72|2*]
A
B [100|2*]

Figure 25. A, strict consensus of ten MPTs of 519 steps with a consistency index (CI) of 0.551 and a retention index (RI) of 0.739 obtained from Wilson's (2002) data matrix; B, strict consensus of 18 MPTs of 678 steps with a CI of 0.472 and an RI of 0.771 obtained from Upchurch *et al*.'s (2004) data matrix. A, Sauropodomorpha; B, Sauropoda; C, Eusauropoda; D, Turiasauria; E, Neosauropoda; F, Diplodocoidea; G, Rebbachisauridae; H, Flagellicaudata; I, Dicraeosauridae; J, Diplodocidae; K, Macronaria; L, Camarasauromorpha; M, Titanosauriforme; N, Somphospondyli; O, Titanosauria; P, Lithostrotia; Q, Saltasauridae. Numbers at nodes indicate bootstrap values and (with asterisk) Bremer support values.

Andesaurus, *Argentinosaurus*, *Lapparentosaurus*, *Nigersaurus*, and '*Pleurocoelus*-tex'. It also incorporated a fixed topology at the base of the cladogram applied in the original analysis (also setting collapse 'rule 3'). The result of the parsimony analysis yielded 18 MPTs with 678 steps and CI = 0.472 and RI = 0.771 (Fig. 25B). The strict consensus follows the main topology obtained in recent publications (Wilson & Upchurch, 2009; Royo-Torres & Upchurch, 2012; Royo-Torres *et al*., 2012).

On the analysis based on the Upchurch *et al*. (2004) data matrix, *Lourinhasaurus* is recovered as a Macronaria, but a single unique synapomorphy of the group (one of three) is available on *Lourinhasaurus*: acute caudal margins of the pleurocoels in the cranial dorsal centra (character 127). This analysis also recovered Camarasauromorpha as a monophyletic group also with three synapomorphies. The inclusion of *Lourinhasaurus* in this clade is supported by the opisthocoelous condition up to the last dorsal vertebrae (character 105) and a ventrally bifurcated or expanded pcdl on middle and dorsal vertebrae (character 142). *Lourinhasaurus*, *Tehuelchesaurus*, and *Camarasaurus* form a monophyletic clade in polytomy, Camarasauridae (*sensu* Taylor & Naish, 2007), that is supported by three synapomorphies: (1) absence of pcpl (character 137); (2) dorsal transverse process directed laterally or slightly upwards (character 138, not preserved in *Lourinhasaurus*); and (3) sternal plate oval or subcircular (character 210). The condition for character 210 is unknown in *Tehuelchesaurus* (Carballido *et al*., 2011).

If *Tehuelchesaurus* is removed a priori from the analyses, the analysis yielded six MPTs with 672 steps and CI = 0.476 and RI = 0.775, and Camarasauridae (*Lourinhasaurus*+*Camarasaurus*) is recovered with improved bootstrap (< 50→60) and Bremer support (1→2) values.

Constrained analyses

Recent studies (e.g. Upchurch *et al*., 2004; Royo-Torres *et al*., 2006, 2009, 2012; Barco, 2010) proposed different phylogenetic positions for *Lourinhasaurus*. Here, we carried out constrained analyses considering *Lourinhasaurus* as: (1) a eusauropod non-neosauropod, (2) a sister taxon of Macronaria, and (iii) a sister taxon of Titanosauriformes. Considering some recent phylogenetic hypotheses (Carballido *et al*., 2011; Carballido & Sander, 2013; Mannion *et al*., 2013), a constrained analysis considering *Tehuelchesaurus* to be a sister taxon of Titanosauriformes was also performed.

These alternative hypotheses of relationships for *Lourinhasaurus* can be accommodated with only a few extra steps, and none can be statistically rejected by the dataset (Table 1). The phylogenetic position of *Lourinhasaurus* near the base of Macronaria is secure, but more robust assessment of its relationships requires new discoveries of more complete specimens of *Lourinhasaurus* and *Tehuelchesaurus*. The introduction of the four *Camarasaurus* species in the cladistic analyses will also be important for the resolution of Camarasauridae, Macronaria, and Camarasauromorpha nodes. Furthermore, the removal of *Tehuelchesaurus* from the present analyses improves significantly the bootstrap and Bremer support values for the Camarasauridae clade. Thus far, our cladistic analysis using the matrix and characters of Wilson (2002) and Upchurch, Barrett & Dodson *et al*. (2004) considers *Lourinhasaurus*, *Camarasaurus*, and *Tehuelchesaurus* as members of a monophyletic clade, Camarasauridae.

DISCUSSION

Lourinhasaurus as a member of Neosauropoda

Lourinhasaurus has several features that support its placement within Neosauropoda. The presence of divided and large pleurocoels in cervical centra, present in *Lourinhasaurus*, is a common feature in neosauropods (character 110, Upchurch *et al*., 2004) that also occurs in some derived eusauropod non-neosauropods such as *Jobaria* (Sereno *et al*., 1999) and *Bellusaurus* (Dong, 1990). *Bellusaurus* was recently recovered as a basal macronarian by Royo-Torres *et al*. (2006) or Carballido & Sander (2013). Among Neosauropoda, the presence of deep and ramified pleurocoels along the dorsal series is common in diplodocoids (excluding Dicraeosauridae, *sensu* Salgado *et al*., 1997) and basal macronarians (Wedel, 2003; Upchurch *et al*., 2004). Some authors also consider this character state to be present in *Bellusaurus*, *Jobaria*, and *Omeisaurus* (Wilson, 2002; Wedel, 2003; Upchurch *et al*., 2004). The dorsal

Table 1. Alternative hypotheses (topological constraints) and Templeton's test results

Constraint	MPTs	Length	Steps	*P*-value	B	BS	Comment	DM
Unconstrained tree	10	519	–	–	< 50	1	–	W
Unconstrained tree without *Tehuelchesaurus*	6	511	–8	–	< 50	2	–	W
Lourinhasaurus + (Macronaria)	1	520	1	0.8185	n.s.	n.s.	Not rejected	W
Lourinhasaurus + (Titanosauriformes)	1	520	1	0.8185	n.s.	n.s.	Not rejected	W
Lourinhasaurus + (Neosauropoda)	49	524	5	0.0588–0.3174	n.s.	n.s.	Not rejected	W
Tehuelchesaurus + (Titanosauriformes)	34	520	1	0.3173–0.8348	n.s.	n.s.	Not rejected	W
Initial constraint based on Upchurch *et al*. (2004) (InC)	18	678	–	–	< 50	1	–	U
InC, without *Tehuelchesaurus*	6	672	–6	–	60	2	–	U
InC, *Lourinhasaurus* + (Macronaria)	3	680	2	0.3173–0.6171	< 50	1	Not rejected	U
InC, *Lourinhasaurus* + (Titanosauriformes)	12	680	2	0.1573–06597	n.s.	n.s.	Not rejected	U
InC, *Lourinhasaurus* + (Neosauropoda)	3	681	3	0.1797–04669	< 50	1	Not rejected	U
InC, *Tehuelchesaurus* + (Titanosauriformes)	6	679	1	0.5637–0.8217	55	1	Not rejected	U

–, not applicable; B, bootstrap value; BS, Bremer support values; DM, data matrix; n.s., not supported; Steps, number of steps more than with the first topology; U, Upchurch *et al*. (2004) data matrix; W, Wilson (2002) data matrix.

bifurcation of the cprl in dorsal vertebrae is considered a synapomorphy of Neosauropoda (Upchurch, Barrett & Dodson, 2004; Carballido *et al*., 2011); the condition is present in *Lourinhasaurus* but absent in some basal titanosauriformes such as *Tastavinsaurus* (Royo-Torres *et al*., 2012), *Giraffatitan* (Janensch, 1950), and *Brachiosaurus* (Riggs, 1903).

Lourinhasaurus also shares with derived eusauropods the presence of five sacral vertebrae (Salgado *et al*., 1997; Wilson & Sereno, 1998; Wilson, 2002; Upchurch *et al*., 2004). The presence of deep excavations on the lateral face of the sacral centrum is a feature with a wide distribution within neosauropods, including diplodocids and macronarians (e.g. Marsh, 1879; Hatcher, 1903; Osborn, 1904; Osborn & Mook, 1921; Janensch, 1950; Salgado, 1993; Curry Rogers & Forster, 2001; Suteethorn *et al*., 2009), but is reversed in some derived titanosaurs (Upchurch, 1998).

The caudal triangular transverse process consists of a short dorsal bar (e.g. Osborn & Mook, 1921; Canudo *et al*., 2008; Gallina & Otero, 2009) that is markedly distinct from the laterally developed transverse process of the caudal vertebrae of diplodocoids and Saltasaurinae (e.g. Lull, 1919; Gallina & Otero, 2009). The simple caudal neural spine is compressed transversely at the base of the spine (this feature is present in *Aragosaurus*, Sanz *et al*., 1987, *Camarasaurus*, Ostrom & McIntosh, 1966, *Giraffatitan*, Janensch, 1950, and *Tastavinsaurus*, Canudo *et al*., 2008) and lacks a complex system of laminae and the transverse development observed in diplodocoids (Wilson, 2002). Flat caudal articulation of proximal caudal vertebrae present in *Lourinhasaurus* is also common in basal macronarians (e.g. *Camarasaurus*, *Tastavinsaurus*, and *Giraffatitan*) and some eusauropods and is distinct from the procoelous proximal caudal centra of flagellicaudatans and titanosaurs (Salgado *et al*., 1997; Upchurch *et al*., 2004; Upchurch & Mannion, 2009) and some non-neosauropods such as *Bellusaurus*, *Chuanjiesaurus*, *Losillasaurus*, and *Mamenchisaurus* (e.g. Young & Zhao, 1972; Dong, 1990; Casanovas, Santafé & Sanz, 2001; Ouyang & Ye, 2002; Sekiya, 2011).

The *Lourinhasaurus* scapula shows several features that are common in neosauropods and sometimes also in members of its stem group (e.g. *Omeisaurus*): (1) an acromion process that is more than 150% the minimum width of the scapular blade; (2) a well-developed and pronounced acromial ridge (Upchurch *et al*., 2004); and (3) the presence of an excavated area behind the acromial ridge (Upchurch *et al*., 2004). The lateral divergence of the preacetabular process of the ilium in dorsal view is generally shared by neosauropods (Wilson & Sereno, 1998). The tibia of *Lourinhasaurus* bears a subcircular proximal articular surface, and the astragalus has a wedge-shaped contour in cranial view, both considered synapomorphies of this clade (Wilson & Sereno, 1998; Wilson, 2002; Upchurch *et al*., 2004).

Lourinhasaurus as a member of Macronaria

Markedly opisthocoelus caudal dorsal vertebrae are synapomorphic for camarasauromorph sauropods (Salgado *et al*., 1997; Upchurch *et al*., 2004) and are convergently shared by a few Chinese eusauropod taxa such as *Mamenchisaurus* (Young, 1954; Young & Zhao, 1972; Ouyang & Ye, 2002) and *Bellusaurus*

(Dong, 1990). The architecture of the middle dorsal neural spine of *Lourinhasaurus* is quite similar to that of some macronarians such as *Camarasaurus* (Ostrom & McIntosh, 1966). The distal transverse expansion of the middle and caudal dorsal neural spines observed in *Lourinhasaurus* and *Camarasaurus* was considered a synapomorphy of Macronaria by Wilson & Sereno (1998). Another feature recognized by D'Emic (2012) as a synapomorphy of the basal macronarian node *Tehuelchesaurus*+Titanosauriformes is the bifurcation of the pcdl in the middle and caudal dorsal vertebrae. This feature has been described in some dorsal vertebrae of *Camarasaurus*, *Tastavinsaurus*, and *Cedarosaurus* (Royo-Torres, 2009), and also observed in *Lourinhasaurus*, suggesting a more widespread distribution among macronarians.

Lourinhasaurus bears a scapular blade with a large distal expansion, a feature that is also observed in basal macronarians such as *Camarasaurus* (e.g. Osborn & Mook, 1921; Ostrom & McIntosh, 1966) and *Giraffatitan* (Janensch, 1961). This feature differentiates *Lourinhasaurus* from Flagellicaudata members with an unexpanded distal scapular blade (e.g. Marsh, 1879, 1881; Osborn, 1904; Lull, 1919; Harris, 2007) and from the greater expansion of the genus *Haplocanthosaurus* (Hatcher, 1903; McIntosh & Williams, 1988) and the distinct racquet-shaped distal expansion exhibited by rebbachisaurids (Salgado *et al*., 2004; Whitlock, 2011).

A humerus with a squared proximal section, i.e. with a break of slope between its proximal and lateral margins that produces an acute or square angle proximolateral border, is variously considered in the literature. Wilson (2002) considered this character a synapomorphy of Somphospondyli (character 159 of Wilson, 2002), while D'Emic (2012) suggested that this feature is a synapomorphy of Macronaria (character 79 of D'Emic, 2012). However, basal macronarians such as *Camarasaurus*, *Tehuelchesaurus*, *Brachiosaurus*, and *Lourinhasaurus* are considered to present the plesiomorphic state, i.e. a rounded transition between the lateral and the proximal edges of the humerus. The co-planar distal ischiatic blade present in *Lourinhasaurus* is also considered a synapomorphy of Macronaria *sensu* Wilson & Sereno (1998). An unexpanded distal end of the ischium distinguishes it from that of diplodocoids such as *Apatosaurus* (Marsh, 1879, 1881), *Barosaurus* (Lull, 1919), *Dicraeosaurus* (Janensch, 1961), and *Diplodocus* (Hatcher, 1901).

One of the forms closest to *Lourinhasaurus* is the macronarian *Camarasaurus*. This was noted earlier by McIntosh (1990a, b), and McIntosh *et al*. (1996b) suggested that the Moinho do Carmo sauropod was a putative new species of *Camarasaurus*, '*Camarasaurus*' *alenquerensis*. Furthermore, some of the *Camarasaurus* autapomorphies (Wilson & Sereno, 1998; Ikejiri, 2004) are shared by *Lourinhasaurus*. If the proposed close phylogenetic relationship between the two species is correct, these shared features have to be considered representative of a more inclusive group, *Lourinhasaurus*+*Camarasaurus*. Among the set of *Camarasaurus* autapomorphies shared by *Lourinhasaurus* are: (1) ischiatic blade directed caudally with its long axis passing through the pubic peduncle (Wilson & Sereno, 1998); and (2) scapular bone with a rounded expansion on the acromial side (Wilson, 2002). Ikejiri (2004) also provides a diagnosis for *Camarasaurus*, some of the features of which are shared by *Lourinhasaurus*, such as a massive pubis with short blade and a tibio-femoral length ratio of ~0.66 (common in several sauropods, see D'Emic *et al*., 2013).

Camarasaurus is one of the best known sauropod genera; it comprises four species (Upchurch *et al*., 2004): *Camarasaurus grandis* (Marsh, 1877), *Camarasaurus lewisi* (Jensen, 1988), *Camarasaurus supremus* Cope, 1877 and *Camarasaurus lentus* (Marsh, 1889). The abundant fossil record of *Camarasaurus* in the Upper Jurassic Morrison Formation has made it possible to identify the existence of great intraspecific variability related to ontogeny, sexual dimorphism, and individual variability (Osborn & Mook, 1921; Ikejiri, 2004; Ikejiri, Tidwell & Trexller, 2005); such analysis has not been possible for other macronarians such as *Tehuelchesaurus*. It is necessary to compare *Lourinhasaurus* with the large range of variability shown by *Camarasaurus* to confirm its relationship with all members of the genus. In addition to the exclusive features supporting the validity of *Lourinhasaurus* and commented on above, there are some particular similarities and differences between the two taxa.

The cervical ventral surface of *Camarasaurus* is considered convex-to-flat transversely (Upchurch *et al*., 2004, character 107; followed by other authors such as Carballido *et al*., 2011), which could suggest a different state than in *Lourinhasaurus*; however, this codification is not sustained by the descriptions of several authors (Osborn & Mook, 1921; Ikejiri, 2004) who describe a concave-to-flat ventral face for *Camarasaurus*, the same condition as is seen in *Lourinhasaurus*. In *Tehuelchesaurus* and *Aragosaurus*, it is not possible to verify this condition (Sanz *et al*., 1987; Carballido *et al*., 2011); however, *Europasaurus* shares this condition with *Lourinhasaurus* and *Camarasaurus* (Carballido & Sander, 2013), and it is also present in *Giraffatitan* (Janensch, 1950) and *Galveosaurus* (Barco, 2009).

Some features of the dorsal vertebrae, especially the neurapophyses system, are diagnostic for

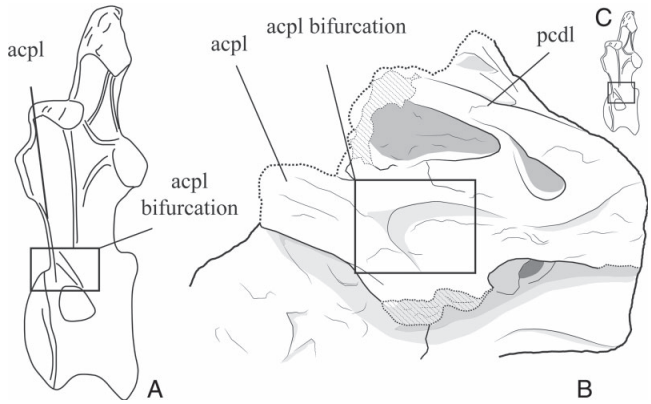

Figure 26. Bifurcated ventral tip in (A) 10th dorsal vertebrae of *Camarasaurus supremus* (Osborn & Mook, 1921: pl. LXX) and (B) DV6 of *Lourinhasaurus alenquerensis* (without scale). Traced line: broken borders; fill in traced pinstripes: broken or eroded areas. C, *Camararasaurus* vertebrae with a box indicating the corresponding region in *Lourinhasaurus* vertebrae.

Camarasaurus (Ikejiri, 2004, 2005). The vertebral centra of *Camarasaurus* and *Lourinhasaurus* show a general likeness, and the topology of pneumaticity is very similar (deep pleurocoels ramifying cranially and caudally). This type of bone tissue is also identified in *Galveosaurus* (considered as a macronarian form by Carballido *et al*., 2011) and *Europasaurus* (Carballido & Sander, 2013). In *Europasaurus*, the pleurocoel becomes less ramified along the vertebral series (Carballido & Sander, 2013), and a similar pattern is observed in *Lourinhasaurus*, reducing the number of smaller cavities connected with the pleurocoels. *Lourinhasaurus* could be distinguished from *Camarasaurus* by the presence of a craniocaudal concavity on the ventral face of the cranial-to-middle dorsal centra; such a concavity is lacking in *Tehuelchesaurus*, *Europasaurus*, and *Haplocanthosaurus* (Hatcher, 1903; Upchurch *et al*., 2004; Carballido *et al*., 2011; Carballido & Sander, 2013).

Several authors consider that the pcdl is not bifurcated or expanded in the caudal dorsal vertebrae of *Camarasaurus* (e.g. Upchurch *et al*., 2004). Nevertheless, the morphology of the pcdl in *Camarasaurus* is variable, and a bifurcated pcdl can be observed in the caudal dorsal vertebrae (e.g. Ostrom & McIntosh, 1966: pl. 25), as was indicated by Royo-Torres (2009). This derived condition is also present in other basal Macronaria such as *Tehuelchesaurus* (Carballido *et al*., 2011), *Tastavinsaurus* (Canudo *et al*., 2008; Royo-Torres, 2009), and *Cedarosaurus* (Royo-Torres, 2009) but absent in *Europasaurus* (Carballido & Sander, 2013). The revision of the *Camarasaurus* laminae system will help in understanding its morphological variability in the time to access a codification in the data matrix. If the pcdl is really bifurcated in *Camarasaurus*, this feature could be a putative synapomorphy of the Camarasauromorpha node. The morphology of the preserved neural spine in *Lourinhasaurus* is similar to that of *Camarasaurus* (e.g. Osborn & Mook, 1921) and represents a unique form among sauropods. The circular depression in the cranial articulation is exclusive to *Camarasaurus* and *Lourinhasaurus*, but in *Camarasaurus* this central depression is neither constant nor circular.

Camarasaurus and *Lourinhasaurus* share a particular feature: the presence of a bifurcation on the ventral tip of the acpl in which the caudal branch develops toward the cranioventral margin of the neural arch, bordering the pleurocoel dorsally (Fig. 26). This feature is also paralleled by other sauropods such as *Tastavinsaurus* (Royo-Torres, 2009, fig. 4.13; R. Royo-Torres, pers. observ., 2013). Other taxa such as *Diplodocus* and *Dinheirosaurus* exhibit a different condition in which the parapophyses are sustained by two laminae, a cranial one (acpl) and a caudal one (pcpl) (Osborn, 1899; Hatcher, 1901; McIntosh & Williams, 1988; Bonaparte & Mateus, 1999; Mannion *et al*., 2012). The presence of pcpl in dorsal vertebrae is recognized in several neosauropods (Wilson, 2002) and in some eusauropods such as *Jobaria* (Sereno *et al*., 1999) and turiasaurs (Royo-Torres *et al*., 2006). The pcpl is absent in *Camarasaurus* and in the preserved dorsal neural arches remains of *Lourinhasaurus*.

In the proximal caudal vertebrae, similarities are also observed in the morphology of the centra and the neurapophyses. These vertebrae share the main centra morphology, the triangular transverse process, and the neural spine morphology. *Lourinhasaurus*

could be distinguished by the presence of a smooth concave ventral face and a less constricted centrum; nevertheless, the interpretation of the caudal vertebrae ventral face is problematic. In character 183 of Upchurch *et al*. (2004) data matrix, the ventral face of *Camarasaurus* proximal caudal vertebrae was codified as transversely convex. By contrast, Ikejiri (2005) described this ventral face as flat, which is similar to the *Lourinhasaurus* state. *Europasaurus* also presents flat to slightly concave ventral faces on the most proximal caudal vertebrae (Carballido & Sander, 2013). The slight ventral concavity present in *Lourinhasaurus* caudals does not resemble the marked concavity common in diplodocoids and in some titanosaurs (Upchurch *et al*., 2004). This situation suggests that it may be necessity to revise the character definition, considering the presence of at least three different states: (1) a clear convex ventral face (the presence of a craniocaudal hollow); (2) a marked concave ventral face; (3) and a flat ventral face (incorporating slight convex and concave states – this state could be identified by a break in the slope between the lateral and ventral faces of the centrum).

The proximal caudal neurapophyses are transversely compressed in both taxa. However, the *Lourinhasaurus* neurapophysis differs from that of *Camarasaurus* by the presence of a circular and deep sprf. The fan-like morphology of the neural spines, in cranial view, is solely shared with *C. grandis* and *C. supremus* (Ikejiri, 2004; Ikejiri *et al*., 2005). Wilson (2002, character 123) accepts the presence of prespinal laminae in *Camarasaurus* proximal caudal spines. Nevertheless, it is herein considered that the cranial surface of the *Camarasaurus* caudal spines bears a shallow and wide prespinal process that is particularly different from the stout and well-defined prespinal lamina present in diplodocids and several titanosauriforms (Salgado *et al*., 1997; Wilson, 1999; Wilson *et al*., 2011). *Lourinhasaurus* and other sauropods such as *Aragosaurus* (Sanz *et al*., 1987), *Spinophorosaurus* (Remes *et al*., 2009), and *Tastavinsaurus* (Canudo *et al*., 2008; Royo-Torres, 2009) also share the presence of a similar wide prespinal process. Wilson (2002, character 124) also refers the presence of a postspinal lamina in the caudal face of the proximal caudal spines of *Camarasaurus*, but the available figures do not confirm the presence of this lamina. *Lourinhasaurus* lacks a postspinal lamina in proximal caudal neural spines.

The subrectangular shape of the scapular distal portion in *Lourinhasaurus* is markedly distinct in most sauropods and is shared only by *Camarasaurus grandis* (Ostrom & McIntosh, 1966) and a specimen of *C. supremus* (BS-179, Ikejiri, 2004). Ikejiri (2004) also noted great intraspecific variability in scapulae of *Camarasaurus* members. The articulation between coracoids and scapulae bears an indentation in *Lourinhasaurus* that does not occur in *Camarasaurus* (Ostrom & McIntosh, 1966; McIntosh *et al*., 1996a). This feature is also observed in *Giraffatitan* (Janensch, 1961) and *Spinophorosaurus* (Remes *et al*., 2009). The *Lourinhasaurus* humeri can be distinguished from the humeri of *C. supremus* (Osborn & Mook, 1921) and *C. lentus* (Ikejiri, 2004) by its more asymmetrical proximal portion (with medially pointed humeral head) and by a lesser value for mediolateral diaphysis/mediolateral proximal portion length. By contrast, the *Lourinhasaurus* humerus shares these conditions with *C. grandis* (e.g. Ostrom & McIntosh, 1966; McIntosh *et al*., 1996b) and *C. lewisi* (McIntosh *et al*., 1996b). McIntosh (1990a, b) suggested the necessity of establishing a new genus based on humerus/femur length ratio, which is higher in *Lourinhasaurus* than in *Camarasaurus*. In fact, the data provided by Ikejiri (2004) show that there is a sub-adult of *Camarasaurus* (*C. lentus*, USNM 13786) with a high humerus/femur length ratio.

The ulna is another distinct bone compared with that of *Camarasaurus*. The *Lourinhasaurus* ulna shares some features with Titanosauriformes (D'Emic, 2012) that are absent in *Camarasaurus* and *Tehuelchesaurus*. One of these features is a caudally unexpanded distal end present in *Lourinhasaurus* and Titanosauriformes. *Camarasaurus* has a marked caudal expansion of the distal ulnar end (Ostrom & McIntosh, 1966) that is shared by several non-Titanosauriformes sauropods (D'Emic, 2012). In proximal view, *Lourinhasaurus* also shows a craniomedial process that is longer and more robust than the craniolateral process. The carpus II of *Lourinhasaurus* is comparably higher than the carpus II of *Camarasaurus* (Osborn, 1904; Ostrom & McIntosh, 1966).

The ilium exhibits some features that are interpreted as distinct from *Camarasaurus*, such as a caudally orientated postacetabular process, a ridge on the ventral margin of the postacetabular process and a small ridge along the ventral margin of the preacetabular process near the pubic peduncle. *Lourinhasaurus* exclusively shares a pronounced caudal deflection of the ischiatic blade with *Camarasaurus*, most precisely with *Camarasaurus grandis* (Ostrom & McIntosh, 1966) (Fig. 20) and *C. lentus* (YPM 1910, McIntoch, 1990b). This caudal deflection is more pronounced than is found in *Aragosaurus* (Sanz *et al*., 1987), *Camarasaurus lewisi* (McIntosh *et al*., 1996b), *C. supremus* (Osborn & Mook, 1921), *C. lentus* (WDC A-BS-9 and WDC BS-615, Ikejiri, 2005), and *Tehuelchesaurus* (Carballido *et al*., 2011). Another particular feature of the ischium is the presence of a lip in the pubic articulation, a feature that is also shared by a specimen of *Camarasaurus supremus* (Osborn & Mook, 1921: fig. 94). Nevertheless, the

absence of this feature in other *C. supremus* ischia suggests the presence of intraspecific variability for this character.

Recent phylogenetic studies are recovering a few classical and new sauropod specimens as basal Macronaria (Sander *et al*., 2006; Carballido *et al*., 2011; Whitlock, 2011; D'Emic, 2012; Carballido & Sander, 2013; Mannion *et al*., 2013). *Haplocanthosaurus*, which is considered by some phylogenetic hypotheses to be a basal macronarian (Wilson & Sereno, 1998; Upchurch *et al*., 2004; Royo-Torres *et al*., 2006; Wilson & Upchurch, 2009; Carballido *et al*., 2011; Carballido & Sander, 2013), can be easily distinguished from *Lourinhasaurus* by the presence of a marked distal expansion of the scapular blade, absence of the opisthocoelous condition up to the sacrals and the presence of pcpl on the dorsal vertebrae (Hatcher, 1903; McIntosh & Williams, 1988). Some recent studies (e.g. Remes *et al*., 2009; Whitlock, 2011) recovered *Haplocanthosaurus* as member of Diplodocoidea.

Europasaurus has recently been considered a basal macronarian in several analyses (e.g. Carballido & Sander, 2013) and is dated to the middle Kimmeridgian, slightly older than *Lourinhasaurus* (late Kimmeridgian to early Tithonian). In addition to its small size, in which it differs from other basal macronarians, it presents distinct aspects compared with *Lourinhasaurus*. One of the most marked differences between the two taxa is morphology of the dorsal neural spines, which have less transversely expanded distal tips and developed pre- and postspinal laminae. *Europasaurus* proximal caudal vertebrae bear a concave caudal articulation (Carballido & Sander, 2013), thus differing from other macronarians with flat-to-concave caudal surfaces such as *Camarasaurus* (Osborn & Mook, 1921), *Lourinhasaurus*, *Brachiosaurus* (D'Emic, 2012), *Haplocanthosaurus* (D'Emic, 2012), *Cedarosaurus* (Tidwell *et al*., 1999), and *Aragosaurus* (Sanz *et al*., 1987). *Tastavinsaurus* has a flat surface that bears a central concavity (Royo-Torres, 2009) as in *Lourinhasaurus*. *Europasaurus* also presents distinct features from *Lourinhasaurus* in its appendicular skeleton. One of the most important differences occurs in the ilium, where *Europasaurus* presents a developed subcircular preacetabular process that is common in the titanosauriformes (Wilson, 2002).

Tehuelchesaurus is a basal macronarian from the Cañadón Calcáreo Formation (Carballido *et al*., 2011), dated as Oxfordian–Kimmeridgian (Cúneo *et al*., 2013). The phylogenetic hypotheses proposed herein suggest a close relationship with *Camarasaurus* and *Lourinhasaurus*, making both taxa a monophyletic clade, Camarasauridae. Nevertheless, *Tehuelchesaurus* can be distinguished in several ways from *Lourinhasaurus* and *Camarasaurus*. *Tehuelchesaurus* can be differentiated from *Camarasaurus* by the absence of a ventrally unbifurcated spol and from *Lourinhasaurus* and *Camarasaurus* in several aspects: (1) lack of distal expansion of the scapular blade, as in the flagellicaudatans (e.g. Marsh, 1879; Ostrom & McIntosh, 1966; McIntosh, 2005; Remes, 2006; Harris, 2007); (2) robust ulna and radius; (3) transversely compressed pubic peduncle; (4) the absence of pronounced ischiatic blade caudal deflection; and (5) femur with subcircular condyles and a slight lateral bulge.

Among the species of *Camarasaurus*, there is great morphological disparity. *Camarasaurus grandis* shares the highest level of similarity with *Lourinhasaurus alenquerensis*. In further analysis, the incorporation and recodification of every *Camarasaurus* species will be necessary to test the relationship of *Lourinhasaurus* with the described species of *Camarasaurus* and to confirm the validity of *Lourinhasaurus* as a valid genus or as a species of *Camarasaurus*, and then to evaluate the implications for *Camarasaurus* palaeobiogeography.

Relationship of *Lourinhasaurus* with Titanosauriformes

Lourinhasaurus does not present several of the synapomorphies of Titanosauriformes. The camellate tissue bone on presacral vertebrae and the pneumatized dorsal ribs present in Titanosauriformes (Wilson & Sereno, 1998; Upchurch *et al*., 2004; Taylor, Wedel & Cifelli, 2011) are absent in *Lourinhasaurus*. On the pelvic girdle, *Lourinhasaurus* also lacks some features commonly shared by titanosauriforms, such as an ischium shorter than the pubis and a rounded preacetabular process with significant craniodorsal development (Upchurch, 1998; Upchurch *et al*., 2004; Royo-Torres, 2009). The massive iliac blade in *Lourinhasaurus* also differs from the thin iliac blade present in several basal Titanosauriformes (e.g. Canudo *et al*., 2008; Royo-Torres, 2009; Taylor, 2009; Taylor *et al*., 2011).

In *Lourinhasaurus*, the femur can be easily distinguished from those of Titanosauriformes by the absence of a bulge in the lateral margin of the femoral proximal section (Salgado *et al*., 1997). *Lourinhasaurus* shows a strong medial deflection of the entire femoral shaft that is considered a different condition from that of basal Titanosauriformes (medial proximal deflection and a lateral bulge, Royo-Torres *et al*., 2012). The 10° deflection of the femoral shaft is slightly higher than is found in *Tastavinsaurus* and *Aragosaurus* (Royo-Torres, 2009; Royo-Torres *et al*., 2012). This combination of a marked deflection of the entire femoral shaft without a lateral bulge is

considered here as autapomorphic for *Lourinhasaurus alenquerensis*. The *Lourinhasaurus* femur also differs from femora that show only a medial proximal deflection, as occurs in other sauropods such as *Apatosaurus* (Marsh, 1881), *Camarasaurus* (e.g. Osborn & Mook, 1921; Ostrom & McIntosh, 1966), *Haplocanthosaurus* (Hatcher, 1903), *Patagosaurus* (Bonaparte, 1979), *Dicraeosaurus* (Janensch, 1961), and *Tornieria* (Remes, 2006). *Saltasaurus* also bears a medial deflection of the entire shaft but with a lateral bulge (Powell, 1992). This evidence suggests that the lateral bulge present in titanosauriforms is independent of the medial displacement of the proximal third of the femur, suggesting a more restricted use of the characters applied to this anatomical region in data matrices (e.g. Wilson, 2002; Upchurch *et al*., 2004; Harris, 2006; Royo-Torres, 2009; Santos, Moratalla & Royo-Torres, 2009; Carballido *et al*., 2011; Royo-Torres *et al*., 2012), following, for example, more restricted character definitions (e.g. Salgado *et al*., 1997).

In a recent analysis (D'Emic, 2012), some diagnostic features of Titanosauriformes that could be observed in *Lourinhasaurus* were discussed. D'Emic (2012) proposed as a synapomorphy of Titanosauriformes a cranial position of the neural arch in the proximal and middle caudal vertebrae, a condition observed in the proximal caudal vertebrae of *Lourinhasaurus*. Despite the presence of a cranial displaced neural arch in the proximal caudal vertebrae of *Lourinhasaurus*, also present in the most proximal caudals of *Camarasaurus* (e.g. Osborn & Mook, 1921; Ostrom & McIntosh, 1966; McIntosh *et al*., 1996a, b) and in other sauropods (e.g. Hatcher, 1901; Casanovas *et al*., 2001; Ouyang & Ye, 2002; Allain & Aquesbi, 2008; Remes *et al*., 2009; Royo-Torres & Upchurch, 2012), this feature could be diagnostic only when is referred to the last proximal caudal vertebrae and middle ones. Therefore, it is not possible to test this condition in *Lourinhasaurus*. Salgado *et al*. (1997), Wilson (2002), and Upchurch *et al*. (2004) used a more restricted definition for this character, considering as synapomorphic of Titanosauriformes the cranial displacement of the neural arches in the middle caudal vertebrae.

D'Emic (2012) also refers to the presence of a ventral process in the base of the scapular blade, a feature that is also present in *Lourinhasaurus*, as a synapomorphy of the Titanosauriformes. The presence of this process in *Mamenchisaurus youngi* Pi, Ouyang & Ye, 1996, *Diplodocus longus* Hatcher, 1901, and *Spinophorosaurus* (Remes *et al*., 2009) suggests the possibility of a convergent acquisition of this character. Following this author, the ulna also bears titanosauriform features such as a caudally unexpanded distal end and a wider and longer cranial process of the proximal surface. *Lourinhasaurus* shares the apomorphic conditions for these characters, suggesting a more derived position with respect to other macronarians such as *Camarasaurus* and *Tehuelchesaurus*.

Taxonomic status of *Lourinhasaurus*

The dorsal cranial vertebrae DV3–DV6 of *Lourinhasaurus* present a marked ventral concavity that is exclusive to this taxon. This feature is lacking in several basal macronarians such as *Haplocanthosaurus* (Hatcher, 1903), *Camarasaurus* (Osborn & Mook, 1921; Ikejiri, 2004), *Tehuelchesaurus* (Carballido *et al*., 2011), *Brachiosaurus* (Riggs, 1903), and *Giraffatitan* (Janensch, 1950). Another relevant character is the circular depression on the cranial articular surface, which is shared only by some *Camarasaurus* specimens. However, in the latter, the depression does not have a marked circular outline and is not constant along the dorsal series.

One of the more distinct features of *Lourinhasaurus* comes from its sacrum. The presence of an acute dorsal termination, producing a craniocaudal crest along the dorsal margin of the sacral spines, and a dorsal projection of the last sacral spines (higher last sacral spines) is particularly unusual in sauropods. This particular morphology could be related to the slight curvature of the sacrum, which results in the articular surface of the last sacral vertebra facing caudodorsally. A similar curvature of the sacrum is also present in *Diplodocus* and *Apatosaurus* (Upchurch *et al*., 2004) and *Tehuelchesaurus* (Carballido *et al*., 2011). This particular structure of the sacral spines is shared by an isolated sacrum (AMNH 690, Osborn, 1904) from Bone Cabin Quarry (CO, USA). This sacrum was historically assigned to '*Morosaurus*' sp. (Osborn, 1904) and now to *Camarasaurus* sp. (Ikejiri, 2004, 2005); it seems to be distinct from several sacra of other *Camarasaurus* specimens (Osborn & Mook, 1921; Ostrom & McIntosh, 1966; McIntosh *et al*., 1996a, b; Ikejiri, 2004; Ikejiri *et al*., 2005). Despite the similarities, the dorsal projection of the last sacral spines is not as pronounced, and the dorsal keel is much more rounded than in *Lourinhasaurus*. As in *Lourinhasaurus*, the postacetabular process also has a caudal orientation in AMNH 690. All other *Camarasaurus* sacrum presents this morphology (Osborn & Mook, 1921; Ostrom & McIntosh, 1966; McIntosh *et al*., 1996a, b; Ikejiri, 2004; Ikejiri *et al*., 2005). The *Lourinhasaurus* ilium exhibits a caudally orientated postacetabular process, a ridge on the ventral margin of the postacetabular process near the ilium peduncle (considered as an autapomorphy) and a small ridge in the ventral margin of the

preacetabular process near the pubic peduncle (Fig. 18B). A caudal orientation of the postacetabular process resembles the plesiomorphic state present in some non-neosauropods such as *Patagosaurus* (Bonaparte, 1986) and *Barapasaurus* (Bandyopadhyay *et al*., 2010) and is an uncommon feature in neosauropods. Thus, this feature cannot be considered an exclusive autapomorphy of *Lourinhasaurus alenquerensis*.

Another exclusive feature of *Lourinhasaurus* is the presence of a well-marked, small, circular and deep sprf on the proximal caudal vertebrae, which is described for *Jobaria* and convergently acquired by this taxon (Sereno *et al*., 1999). In *Camarasaurus*, *Tastavinsaurus*, and *Aragosaurus*, when such an sprf is present, it shows a dorsoventral elongated morphology (e.g. Osborn & Mook, 1921; Sanz *et al*., 1987; Canudo *et al*., 2008; Royo-Torres, 2009; Wilson *et al*., 2011).

In *Lourinhasaurus*, carpal II shows a circular process in the distal surface that is undescribed in other sauropods. This feature could be considered a putative autapomorphy of *Lourinhasaurus alenquerensis*; nevertheless, because the carpal bones are not preserved in most sauropod specimens, it should be taken with caution.

The *Lourinhasaurus* pubis shows an acute cranioventral corner of the distal end, a feature that has only been identified in *Tastavinsaurus* and was previously considered an autapomorphy of this taxon (Canudo *et al*., 2008). The phylogenetic hypothesis herein proposed suggests that this may be due to a process of convergence. Another particular feature that distinguishes the *Lourinhasaurus* pubis from that of other sauropods is the parallelization of the pubic axis and its ischiatic articulation. In the ischia, the acetabulum surface is bordered by a marked ridge and groove, another diagnostic feature that is exclusive to *Lourinhasaurus alenquerensis*. As was indicated above, a whole femoral shaft deflection without a break of slope is also exclusive to this taxon. The femur of *Lourinhasaurus* also bears a femoral head with a great lateromedial length and short proximodistally width, uncommon features for sauropods. Similar fibular and tibial length is also particularly unusual in sauropods, in which the fibula is generally longer than the tibia for the reception of the astragalus lateral surface. This feature is considered exclusive for this taxon.

Comparison with Upper Jurassic to basal Lower Cretaceous Iberian sauropods

The consideration of *Lourinhasaurus* as a basal Macronaria supports the previous assignment of some Portuguese Upper Jurassic sauropods to Macronaria, such as an incomplete caudal series from the tithonian beds of Praia de Areia Branca (Lourinhã, Portugal) (Yagüe *et al*., 2006). In addition to the presence of this member of Macronaria, Portuguese Upper Jurassic sauropod fauna also include other taxa such as *Dinheirosaurus* and *Lusotitan*. *Dinheirosaurus* is considered a diplodocid (Bonaparte & Mateus, 1999; Mannion *et al*., 2012). It clearly differs from *Lourinhasaurus* in bearing a caudal concavity on the ventral face of the first six dorsal centra and a ventral keel in the first and, weakly, in the second one (Mannion *et al*., 2012). *Lourinhasaurus* presents a marked ventral concavity in DV3–DV6 that is bordered by smooth craniocaudal crests and lacks a sagittal ventral keel. Other differences identified in *Dinheirosaurus* are: (1) the absence of eprl in the caudal cervical neural spines; (2) the presence of typical diplodocid dorsal neural spines; (3) a cranial pleurocoel with rounded caudal margin; (4) the presence of pleurocoels on the proximal caudal vertebrae; and (5) the absence of an opisthocoelous condition of the dorsal centra up to the sacral vertebrae. A putative second diplodocid found at Moita dos Ferreiros at Lourinhã (Mannion *et al*., 2012) also shows several differences from *Lourinhasaurus*, particularly in the morphology of the neural arches (e.g. the rectangular profile of the spines in caudal view and the presence of bulbous dorsal processes).

Lusotitan atalaiensis is usually considered a basal titanosauriform (Antunes & Mateus, 2003). A recent first cladistic analysis supports *Lusotitan* as a basal Macronaria that could be related to Brachiosauridae with doubts (Mannion *et al*., 2013). *Lusotitan* differs from *Lourinhasaurus* in several ways, such as dorsal and caudal centra that are dorsoventrally compressed, a radius longer than the tibia, and a pronounced and proximodistally restricted deltopectoral crest.

In addition to the neosauropod representatives of the Portuguese Upper Jurassic, there are several remains, primarily teeth and post-cranial material that have been related to the non-neosauropod group Turiasauria, together with several Spanish taxa from the Upper Jurassic to Lower Cretaceous transition (Royo-Torres *et al*., 2006, 2009; Mateus, 2009; Ortega *et al*., 2010; Mocho, Ortega & Royo-Torres, 2012). *Lourinhasaurus* differs from Turiasauria members (*Turiasaurus*, *Losillasaurus*, and *Galveosaurus*) in several aspects (Royo-Torres *et al*., 2006, 2009; Royo-Torres & Upchurch, 2012). *Turiasaurus* and *Galveosaurus* could be distinguished from *Lourinhasaurus* by the dorsally unbifurcated cprl on the middle and caudal dorsal vertebrae and the flat surface caudal to the acromial crest (Royo-Torres *et al*., 2006). The tibia of *Turiasaurus* presents important differences from that of *Lourinhasaurus*,

bearing some plesiomorphic states not present in non-titanosauriform neosauropods, a transversely compressed proximal section and a craniolaterally orientated cnemial crest. *Losillasaurus* is easily distinguished by the presence of unbifurcated cervical neural spines, non-opisthocoelous caudal dorsal centra, and strong procoelous proximal caudals with a longer ratio (greater than 0.6) of centrum length to centrum height (Casanovas *et al*., 2001). *Turiasaurus*, *Losillasaurus*, and *Galveosaurus* pleurocoels have rounded caudal margins (Royo-Torres *et al*., 2006), a condition different from the acute margins observed in *Lourinhasaurus* and *Camarasaurus* cranial dorsal vertebrae. *Lourinhasaurus* also differs from the turiasaurs by the presence of divided cervical pleurocoels, the absence of a pcpl, the absence of a strongly concave lateral margin on the sternal plates in ventral view, and an unpronounced deltopectoral crest.

Aragosaurus bears similar morphological aspects to *Lourinhasaurus* in the pubis, humerus, and ischium (Sanz *et al*., 1987; Royo-Torres, Canudo & Ruiz-Omeñaca, 1999). Nevertheless, *Aragosaurus* presents some differences, including a less caudally deflected ischiatic blade and the presence of a lateral bulge in the femur; furthermore, the sprf is not circular as in the proximal caudal vertebrae of *Lourinhasaurus*.

Despite its similarity to *Camarasaurus*, *Lourinhasaurus* represents an exclusive form, as occurs with other Iberian contemporaneous sauropods (Dantas *et al*., 1998; Bonaparte & Mateus, 1999; Casanovas *et al*., 2001; Antunes & Mateus, 2003; Sánchez-Hernández, 2005; Royo-Torres *et al*., 2006). The putative exclusivity of the Upper Jurassic sauropods of the Iberian Peninsula does not support the proposal of faunal contacts with North America during the later part of the Late Jurassic that is suggested by the amphiatlantic distribution of genera and species of other theropods, ornithopods, and stegosaurs (Galton, 1980; Pérez-Moreno *et al*., 1999; Mateus & Antunes, 2000a, b; Mateus, 2006; Mateus, Walen & Antunes, 2006; Ortega *et al*., 2006, 2009; Escaso *et al*., 2007; Malafaia *et al*., 2007, 2010), plants (Mohr, 1989), mammals (Martin, 2000), and ostracods (Schudack, 2000). However, the referred presence of a sacrum from the Bone Cabin Quarry (Morrison Formation; lower Kimmeridgian) (Osborn, 1904) sharing exclusive features with *Lourinhasaurus* suggests the presence of forms closely related to this genus that must be evaluated when new material becomes available. Despite the apparent isolation between Portuguese and North America Upper Jurassic sauropod faunas, the identified taxa belong to the same main groups of sauropods such as diplodocids, camarasaurids, and brachiosaurids.

The status of Camarasauridae

The phylogenetic hypotheses proposed herein suggest the existence of a clade that includes *Camarasaurus*, *Lourinhasaurus*, and probably *Tehuelchesaurus*. This clade corresponds to all sauropods more closely related to *Camarasaurus* than to *Saltasaurus*, defined by Taylor & Naish (2007) as Camarasauridae. Unfortunately, putative important diagnostic elements for Camarasauridae affinities are missing in *Lourinhasaurus* and *Tehuelchesaurus*. In the case of *Lourinhasaurus*, the lack of a complete axial skeleton makes an accurate comparison with the diagnostic neurapophyseal systems of *Camarasaurus* and *Tehuelchesaurus* impossible. *Lourinhasaurus* and *Tehuelchesaurus* also lack the cranial remains that are available for *Camarasaurus* (e.g. Osborn & Mook, 1921; Ostrom & McIntosh, 1966; McIntosh *et al*., 1996a, b; Zheng, 1996).

As mentioned above, some autapomorphies traditionally diagnostic for *Camarasaurus* are also shared by *Lourinhasaurus* (e.g. cranial deflection of the ischiatic blade); these could be synapomorphies of the herein proposed Camarasauridae clade. *Tehuelchesaurus* exhibits some plesiomorphies with respect to *Camarasaurus* and *Lourinhasaurus*, such as the absence of triangular processes of the dorsal neural spines and an unexpanded distal end of the scapular blade. There are also remarkable differences between the appendicular elements of *Tehuelchesaurus* (the ulna, radius, and pelvic girdle) and those of *Camarasaurus* and *Lourinhasaurus*.

Indeed, distinct phylogenetic positions have been proposed for *Tehuelchesaurus* in recent cladistic analyses, indicating an unstable position. *Tehuelchesaurus* has been considered a eusauropod closely related to *Omeisaurus* (Upchurch *et al*., 2004), a basal camarasauromorph more derived than *Camarasaurus* (Carballido *et al*., 2011; D'Emic, 2012), of uncertain relationship with *Galveosaurus* (Carballido *et al*., 2011) or *Tastavinsaurus* (Carballido & Sander, 2013), and even a macronarian more primitive than *Camarasaurus* (Mannion *et al*., 2013).

Palaeobiogeography of Macronaria during the Late Jurassic

At present, knowledge of the non-titanosauriform macronarians is relatively poor, but recent cladistic work has begun to re-analyse the traditional assignment of several sauropod specimens to Macronaria and Camarasauromorpha, resulting in new palaeobiogeographical hypotheses (e.g. Carballido *et al*., 2011; Carballido & Sander, 2013; Mannion *et al*., 2013). Unfortunately, the phylogenetic relationships of the putative stem groups or basal forms of these two clades are poorly known (e.g. *Abrosaurus*,

Ouyang, 1989) or are unstable, as is the case for *Haplocanthosaurus* (e.g. Wilson & Sereno, 1998; Wilson, 2002; Upchurch *et al*., 2004; Carballido *et al*., 2011), *Galveosaurus* (see Barco, 2010; Carballido *et al*., 2011; D'Emic, 2012; Royo-Torres & Upchurch, 2012; Royo-Torres *et al*., 2012), *Bellusaurus* (e.g. Upchurch *et al*., 2004; Royo-Torres & Upchurch, 2012; Royo-Torres *et al*., 2012), and *Jobaria* (Sereno *et al*., 1999; Wilson, 2002; Upchurch *et al*., 2004). This instability has important implications for our knowledge of the origin of the neosauropods, of the basal dicahotomy between Diplodocoidea and Macronaria, and, consequently, of the paleobiogeography of those groups (also noted by Carballido *et al*., 2011).

Considering the hypothesis proposed herein and other recent phylogenetic hypotheses, it is possible to consider a widespread distribution of basal non-titanosauriform macronarians in the Upper Jurassic consisting of laurasiatic and gondwanic forms. From North America, there are four taxa: *Camarasaurus grandis*, *C. lewisii* (which could be synonymous of *C. grandis sensu* Ikejiri, 2005), *C. supremus*, and *C. lentus. Haplocanthosaurus* is a genus comprising two species: *H. priscus* Hatcher, 1903 and *H. delfsi* McIntosh & Williams, 1988. As was noted above, the phylogenetic position of *Haplocanthosaurus* is uncertain, being recovered as a basal macronarian in some phylogenetic hypothesis (e.g. Wilson & Sereno, 1998; Upchurch *et al*., 2004; Royo-Torres *et al*., 2006; Carballido & Sander, 2013). Nevertheless, *Haplocanthosaurus* has been recovered outside of Macronaria by several phylogenetic hypotheses (e.g. Wilson, 2002; Harris, 2006; Remes, 2006; Remes *et al*., 2009; Royo-Torres *et al*., 2009, 2012; Whitlock, 2011; Royo-Torres & Upchurch, 2012). Furthermore, Calvo & Salgado (1995) suggested that *Haplocanthosaurus* could be paraphyletic, with *H. priscus* more related to Diplodocoidea. From Eurasia, *Lourinhasaurus* and *Europasaurus* are the only basal macronarians identified at present (Sander *et al*., 2006; Carballido & Sander, 2013; this work). Some authors considered *Europasaurus* as a member of the Brachiosauridae (D'Emic, 2012; Mannion *et al*., 2013). Barco (2010) and Carballido *et al*. (2011) considered *Galveosaurus* to be a basal macronarian; nevertheless, this position is not herein supported. Other phylogenetic hypotheses considered *Galveosaurus* to be a non-neosauropod eusauropod member of the Turiasauria clade (Royo-Torres *et al*., 2006, 2009; Royo-Torres & Upchurch, 2012; Royo-Torres *et al*., 2012), a diplodocoid (Barco *et al*., 2005), a 'cetiosaurid' (Sánchez-Hernández, 2005), or a titanosauriform (D'Emic, 2012). *Aragosaurus* was considered a camarasaurid and was originally dated as probably of Hauterivian? (Sanz *et al*., 1987) or Valanginian?–Hauterivian age (Canudo *et al*., 2012). Nevertheless, some authors proposed a Tithonian–Berriasian age for *Aragosaurus* (Alcalá *et al*., 2009; Royo-Torres *et al*., 2009; Cobos & Gascó, 2013); therefore, it could also be referred as an Eurasiatic Upper Jurassic basal macronarian, in addition to *Lourinhasaurus* and *Europasaurus*.

Tehuelchesaurus is recovered here as a basal Macronaria, a phylogenetic result already proposed by Carballido *et al*. (2011), D'Emic (2012), and Mannion *et al*. (2013). This approach expands the palaeobiogeographical distribution of basal non-titanosauriforms along the Upper Jurassic to South America. Mannion *et al*. (2013) also considered as members of Macronaria several sauropod remains from the Upper Jurassic of the Cañadón Calcáreo Formation in Chubut, Argentina, first assigned to Titanosauriformes by Rauhut (2006), an assignation recently supported by D'Emic (2012).

From the Tendaguru beds of the Upper Jurassic are taxa that are occasionally considered Macronaria members, such as *Janenschia* and *Tendaguria* (e.g. Carballido *et al*., 2011); however, *Janenschia* type specimens represent a different type of sauropod (Bonaparte *et al*., 2000; Royo-Torres & Cobos, 2009). D'Emic (2012) considered *Janenschia* as a member of Titanosauriformes. As was discussed above, the assignment of *Abrosaurus* and *Bellusaurus* to Macronaria is problematic. Recently, Carballido & Sander (2013) recovered *Bellusaurus* as a member of Camarasauromorpha, suggesting the presence of camarasauromorphs during the Late Jurassic in East Asia. If eusauropod non-neosauropod placement of *Bellusaurus* is supported, no other Macronaria sauropod is recognized in East Asia territory during the Late Jurassic. Furthermore, the absence of Macronaria in East Asia during the Late Jurassic could be sustained by the proposed isolation of this territory at the Middle Jurassic to Lower Cretaceous boundary, resulting in the development of endemic faunas (e.g. Milner & Norman, 1984; Upchurch, 1995; Barrett *et al*., 2002; Wilson & Upchurch, 2009).

Lourinhasaurus increases the known diversity of basal macronarians in the European Upper Jurassic. The widespread distribution of non-titanosauriforms macronarians (Europe, North America, South America, and putatively Africa) fits with the wide distribution of diplodocoids (North America, Africa, and Europe), titanosauriforms (North America, Africa, Europe, and putatively South America; Carballido *et al*., 2011; D'Emic, 2012) and probably turiasaurs (Europe and Africa; Royo-Torres & Cobos, 2009; Royo-Torres *et al*., 2009) during the Late Jurassic.

CONCLUSIONS

The revision of the *Lourinhasaurus alenquerensis* lectotype (including some material referred by Lapparent & Zbyszewski, 1957, but not considered in the original *Lourinhasaurus alenquerensis* diagnosis by Dantas *et al*., 1998) permits the development of a new phylogenetic approach. The phylogenetic hypotheses proposed herein consider *Lourinhasaurus* as a basal member of Macronaria and as a basal camarasauromorph. The analysis also allows the recognition of Camarasauridae as a monophyletic clade that gathers *Lourinhasaurus*, *Camarasaurus*, and *Tehuelchesaurus*. In spite of the morphological similarities between *Camarasaurus* and *Lourinhasaurus*, it is considered that *Lourinhasaurus alenquerensis* is distinct from known *Camarasaurus* species on the basis of several anatomical features, including a few exclusive features. Some previously considered diagnostic features of *Camarasaurus*, such as the pronounced caudal deflection of the ischiatic blade and the presence of a rounded expansion on the acromial side of the scapula, are herein proposed as synapomorphies of a more inclusive group that includes *Lourinhasaurus* and *Camarasaurus*. Further phylogenetic reassessment of the genus *Camarasaurus* that involves the consideration of every *Camarasaurus* species will indicate the position of *Lourinhasaurus* with respect to the members of this genus.

Lourinhasaurus alenquerensis is considered here as an exclusive taxon of the Iberian Upper Jurassic like *Lusotitan*, *Dinheirosaurus*, *Galveosaurus*, *Losillasaurus*, *Turiasaurus*, or, if its Late Jurassic age is confirmed, *Aragosaurus*. The existence of this sauropod fauna suggests high diversity in the Iberian Peninsula during the Late Jurassic, similar to the diversity documented in other formations of similar ages, i.e. Morrison and Tendaguru, and does not support the hypothesis of a connection between North America and the Iberian Peninsula faunas during the later part of Late Jurassic reflected by other faunal and floral groups.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Measurements for *Lourinhasaurus alenquerensis*.
Appendix S2. Map of synapomorphies.
Appendix S3. Data matrix.

CHAPTER 11

New data for the Portuguese brachiosaurid *Lusotitan atalaiensis* (Sobral Formation, Upper Jurassic)

New data for the Portuguese brachiosaurid *Lusotitan atalaiensis* (Sobral Formation, Upper Jurassic)

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11.1. INTRODUCTION

In 1947 M. de Matos and P. Carreira de Deus found a new sauropod specimen in Atalaia (Lourinhã municipality) that was published with other fragmentary material from Areia Branca, Porto Novo, Cambelas and Praia das Almoinhas as a new taxon by Lapparent and Zbyszewski (1957). The Atalaia specimen was firstly related to *Brachiosaurus* genus (in that time also including the African taxon, *Giraffatitan*), assignation that was mainly based on similarities with the *Brachiosaurus* limbs. Besides the similarities between the Portuguese specimen and the North American one (*Brachiosaurus altithorax* Riggs, 1903), comparing with the more complete material of *Giraffatitan brancai* Janensch, 1936 (considered as member of the *Brachiosaurus* genus in that time), Lapparent and Zbyszewski (1957) established a new species of *Brachiosaurus*, *B. atalaiensis*. This new species was established taking into account the differences shown by the cervical vertebrae (reinterpreted here as an incomplete sacral centrum) and the limb bones of Atalaia specimen when compared with *Giraffatitan*. Janensch (1961) also noted for the similarities between *B. atalaiensis*, *G. brancai* and *B. altithorax*. McIntosh (1990a) considered desirable new material to obtain a more precise taxonomic approach, however, he noted for the similarities between the caudal vertebrae of Portuguese specimen and *Brachiosaurus*. Upchurch et al. (2004) do not identify any *Brachiosaurus* synapomorphy features on Portuguese specimen and noted for the differences between the ischia of both taxa, more steeply inclined in *Brachiosaurus*, i.e. in *Giraffatitan* ischia. These authors referred the Portuguese taxon as a Brachiosauridae *incertae sedis*.

From the type material of *Brachiosaurus atalaiensis*, Antunes and Mateus (2003) established new generic taxa, *Lusotitan*. These authors considered it as a member of Brachiosauridae due a set of synapomorphies such as the presence of lower neural spines, a pronounced deltopectoral crest, an elongated humerus and a dorsally directed longitudinal axis of the ilium (see diagnosis in Antunes and Mateus, 2003).

The incompleteness of the type specimen of *Lusotitan atalaiensis* difficults to provide an accurate phylogenetic placement for *Lusotitan atalaiensis*. Recently, some authors suggested different phylogenetic assignations but not based in cladistics analyses. For example, Carrano (2005) relates *Lusotitan* to basal Macronaria, assignation followed by Carballido et al. (2011). Royo-Torres (2009) and Canudo et al. (2009) referred *Lusotitan* as a titanosauriform. D'Emic (2012) also supported that hypothesis considering *Lusotitan* as a derived member of brachiosaurids, a titanosauriform group, which includes *Abydosaurus*, *Brachiosaurus*, *Cedarosaurus*, *Giraffatitan* and *Europasaurus*. Most recently, Mannion et al. (2013) redescribed some elements of the type specimen of *Lusotitan atalaiensis*, proposing a new diagnosis and one of the first cladistic analysis for this taxon, recovering it as a basal Macronaria, member of Brachiosauridae with doubt.

In this study, new data for *Lusotitan* is provided with the description and redescription of some elements of the *Lusotitan* lectotype specimen housed in Museu Geológico. It also proposed an emended diagnosis for *Lusotitan atalaiensis*. In order to obtain a new phylogenetic approach for the fragmentary taxon *Lusotitan* we provide few phylogenetic hypotheses based on several published data matrix. Finally it will be discussed the paleobiogeographical implications of *Lusotitan* for the understanding of sauropods faunas around the proto North-Atlantic during the Upper Jurassic.

11.2. GEOLOGICAL SETTINGS

The described remains were collected north of Lisboa, in the Atalaia locality (Lourinhã municipality) near the cliffs of Peralta (Fig. 11.1a). The sedimentary sequence outcropping in Peralta fits within an Upper Jurassic to Lower Cretaceous sequence deposited in the Lusitanian Basin during the third rifting episode (Rasmussen et al., 1998; Kullberg et al., 2006). This period is characterized by internal differentiation in several sub-basins and important siliciclastic inputs

that progressively infilled these basins (Pena dos Reis et al., 2000). Since the Kimmeridgian, the sedimentary sequence is marked by a strong siliciclastic nature, with a continental signature in the top of sequence (Hill, 1988).

The Peralta quarry are located in the Bombarral Sub-basin (Guéry, 1984) where outcrops sediments referred as "Pterociano" by Camarate França et al. (1961) and, more recently, referred to Sobral Formation (e.g. Manuppella et al., 1999) (Fig. 11.1b). The Sobral Formation is interpreted as the result of sedimentation in an estuarine delta complex (e.g. Leinfelder, 1993; Kullberg et al., 2006) dated from upper Kimmeridgian-to-lower Tithonian (Fürsich, 1981) (Fig. 11.1c). Sobral Formation is rich in fossil vertebrate remains highlighting the type specimens of the camarasauromorph *Lourinhasaurus alenquerensis* (Lapparent and Zbyszewski, 1957) or the theropod *Lourinhanosaurus antunesi* Mateus, 1998. Fossils attributed to neopterygians, turtles, crocodyliforms, and dinosaurs were collected from the Peralta quarry.

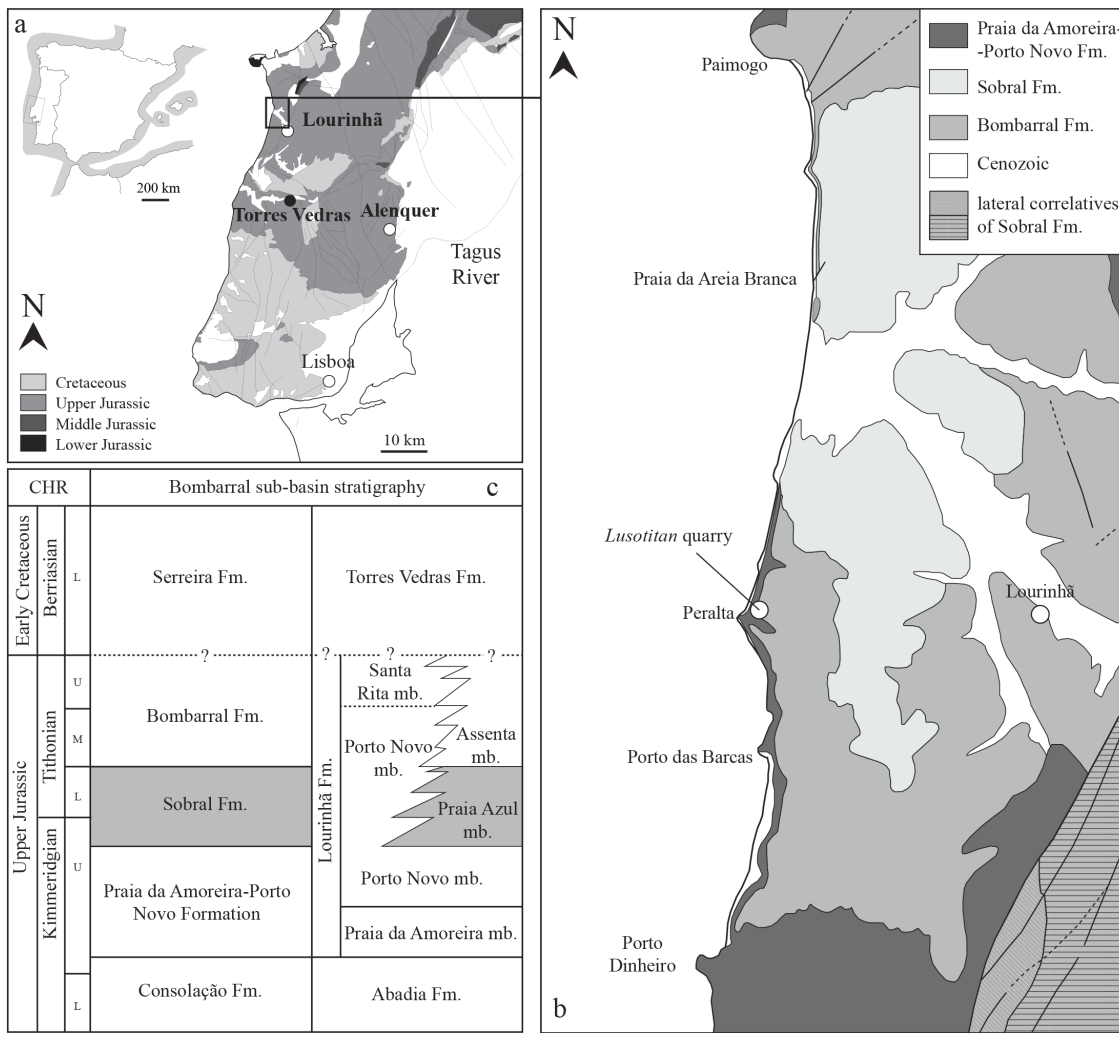

Figure 11.1. a) Geological map (adapted from Oliveira et al., 1992) showing the Portuguese Mesozoic levels; b) Geological map of the Lourinhã region (adapted from Manuppella et al., 1999) with the location of Peralta site; c) Stratigraphy of Bombarral sub-basin sensu Manuppella et al. (1999) and Hill (1988), CHR – Chronostratigraphy.

11.3. INSTITUTIONAL ABBREVIATIONS

FMNH, Field Museum of Natural History, Chicago, USA; MG, Museu Geológico do Laboratório Nacional de Energia e Geologia, Lisboa, Portugal; NHMUK, Natural History Museum, London, UK.

11.4. ANATOMICAL ABBREVIATIONS

ap, anterior process; acet, acetabulum; asp, ascending process; aspa, articular surface for ascending process, at: anterior trochanter, cc, cnemial crest; lat. cpol, lateral centropostzygapophyseal lamina; dpc, deltopectoral crest; fia, fibular articular surface; hyp, hyposphene; ilped, iliac peduncle; lat. Sprl, lateral spinopostzygapophyseal lamina; lf, lateral fossa; lt, lateral trochanter; med. Sprl, medial spinopostzygapophyseal lamina; mp, medial process; mv, medial view; isped, ischial peduncle; ns, neural spines; of, obturator foramen; ol, olecranon; paf, posterior astragalus fossa; pafc, crest in posterior astragalar fossa; pl, pleurocoelus; posl, postspinal lamina; poz, postzygapophyses; pped, pubic peduncle; prdl, prezygodiapophyseal lamina; prsl, prespinal lamina; prz, prezygapophyses; pvp, posteroventral process; sdf, spinodiapophyseal fossa; raf, radial fossa; spdl, spinodiapophyseal lamina; spol, spinopostzygapophyseal lamina; spof, spinopostzygapophyseal fossa; sprl, spinopostzygapophyseal lamina, sprf, spinoprezygapophyseal fossa, sym, symphyses; tp, transverse process (sacral rib or caudal rib, *sensu* Wilson 2012); tia, tibial articulation; ump, ulnar medial process; uclp, ulnar anterolateral process.

11.5. SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1841
Saurischia Seeley, 1887
Sauropoda Marsh, 1878
Neosauropoda Bonaparte, 1986
Macronaria, Wilson and Sereno, 1998
Titanosauriformes Salgado et al., 1997
Lusotitan Antunes and Mateus, 2003

Type species: *Lusotitan atalaiensis* (Lapparent and Zbyszewski, 1957)

Diagnosis: As for type and only known species.

Lusotitan atalaiensis (Lapparent and Zbyszewski, 1957)

1957 *Brachiosaurus atalaiensis* Lapparent and Zbyszewski, 1957, p. 33
2003 *Lusotitan atalaiensis* (Lapparent and Zbyszewski): Antunes and Mateus, 2003, p. 82.
2013 *Lusotitan atalaiensis* (Lapparent and Zbyszewski): Mannion et al., 2013

Etimology: *Lusotitan*, *Luso*, from an inhabitant of Lusitania, an ancient region of the Portugal; *titan*, from the Greek word for a mythological giant; *atalaiensis*, from Atalaia, a locality of Lourinhã municipality (northern of Lisboa) where were found the lectotype of this taxon.

Lectotype: Since Lapparent and Zbyszewski (1957) not assigned holotype, Antunes and Mateus (2003) established as lectotype one of the individuals originally referred to this taxon. Both, Antunes and Mateus (2003) and Mannion et al. (2013) provided a list of elements of the lectotype. However, as result of the current review, a new list that has some variations is proposed. The type material corresponds to a unique individual and is composed by a middle-to-posterior dorsal vertebra (MG 4985-1), dorsal rib fragments (MG 5795, MG 8793), one sacral vertebra (MG 4801), two sacral spines (an unlabeled sacral neural spine and MG 8807), one sacral rib (MG 4798), 19

caudal vertebrae (MG 4985 2-20), several chevrons (an unlabeled anterior chevron and MG 4805-10); left (MG 4944) and right (MG 4989) humerus, left ulna (MG 4966), left (MG 4950) and right (MG 4958) radii; left pubis (MG 4965), left ischium (MG 4952), left tibia (MG4981), left fibula (MG 4982) and left astragalus (MG 4803). It also identified several fragments (MG 8794, 4838) including a plate-like fragment assigned to the ilium (MG 4938), considered here has an indeterminate fragment, and other indeterminate fragments (MG 8794).

Emended diagnosis (*exclusive of *Lusotitan*): (1) spdl does not reach the distal process on sacral neural spines*; (2) small lateral projection of spol at midheight of the most anterior sacral spine*; (3) the caudal rib on the anteriormost caudal vertebra is convex dorsolaterally in posterior view (*sensu* Mannion et al., 2013); (4) anterior-to-middle caudal postzygapophyses transversely compressed, constituting elongate processes that project well beyond the posterior margin of the neural arch (*sensu* Mannion et al., 2013); (5) the presence of transverse elongated or T-shaped pits in the middle caudal vertebrae* (modified from Mannion et al., 2013); (6) circular fossae in the ventral face of the middle caudals, anteriorly located to the chevron facets (new); (7) presence of proximal bridged chevrons (new); (8) short ischiatic peduncle (new); (9) pubis blade with a marked anterior orientation (new); (10) anterior margin of pubis peduncle bearing a rounded projection (new); (11) pubis peduncle of the ischium constricted in anterior view* (new); (12) tibia strongly bowed laterally (*sensu* Mannion et al., 2013); (13) no vertical groove extending up the shaft between the lateral and medial malleoli of the tibia (*sensu* Mannion et al., 2013); (14) tibial crest ventrally directed* (new); (15) acute lateral margin of the tibia, bordered by dorsoventral smooth grooves (new); (16) abrupt transition between the dorsal surface of the articular surface of ascending process and the lateral surface of the tibial shaft* (new).

Site and horizon of the lectotype: Peralta, near Atalaia locality on Lourinhã municipality, northeast of Lisboa. Sobral Formation, upper Kimmeridgian-lower Tithonian, Lusitanian Basin (Manuppella et al., 1999).

11.5.1. Description

Herein it is proposed a detailed description for previously undescribed bones and new interpretations for some elements belonging to the lectotype of *Lusotitan*. It was possible to reassess *in situ*, in Museu Geológico collections, almost all elements previously referred to *Lusotitan* type specimen (Lapparent and Zbyszewski, 1957; Antunes and Mateus, 2003). However, some of them were not identified neither quoted in Museu Geológico facilities such as one of the previously referred cervical vertebrae by Lapparent and Zbyszewski (1957), some dorsal rib fragments, scapulae and sternum remains. The element figured as an ilium (MG 4958) by Antunes and Mateus (2003) and Mannion et al. (2013) corresponds to an indeterminate element without any feature assignable to an ilium. This element corresponds to a bone plate, which deflects in the region identified as ischiatic peduncle by these authors. If this interpretation is accepted, the preacetabular process should deflect medially, which is particularly unusual for a sauropod. The identified ischiatic peduncle does not bear any feature for articulation. This element might be a sternal plate, but only future material could confirm this anatomical assignment. Besides the reference of an ilium by Lapparent and Zbyszewski (1957), no available element among the type material of *Lusotitan atalaiensis* can be assigned to an ilium.

Dorsal vertebra: Only one posterior-to-middle dorsal centrum is preserved (Fig. 11.2) and for a detailed description see Mannion et al. (2013). As referred Mannion et al. (2013), the anterior face is not well-preserved, but seems to bear a particular condition, a slight convexity (like a lip structure) in the dorsal region which deflects posteriorly producing a slight concave-to-flat surface, similar condition observed in the most posterior dorsal centrum of *Brachiosaurus* (Riggs, 1903). Nevertheless, the middle-to-posterior dorsal vertebrae in both taxa are considered

as opisthocoelous in the present phylogenetic analyses (character #105 in Wilson (2002) and Upchurch et al. (2004) data matrices). The pleurocoels are ventrally deep and occupying 2/3 of the anteroposterior length of lateral face of the centrum (Fig. 11.2c). Mannion et al. (2013) referred that the pneumatic cavities are ramified, however, that is not possible to confirm it due the state of preservation of the internal morphology of the pleurocoel. The internal texture of the bone is hard to describe, however, between the anterior face and the neural arch, where the centrum is fractured, it is possible to observe that several cameras compose the bone.

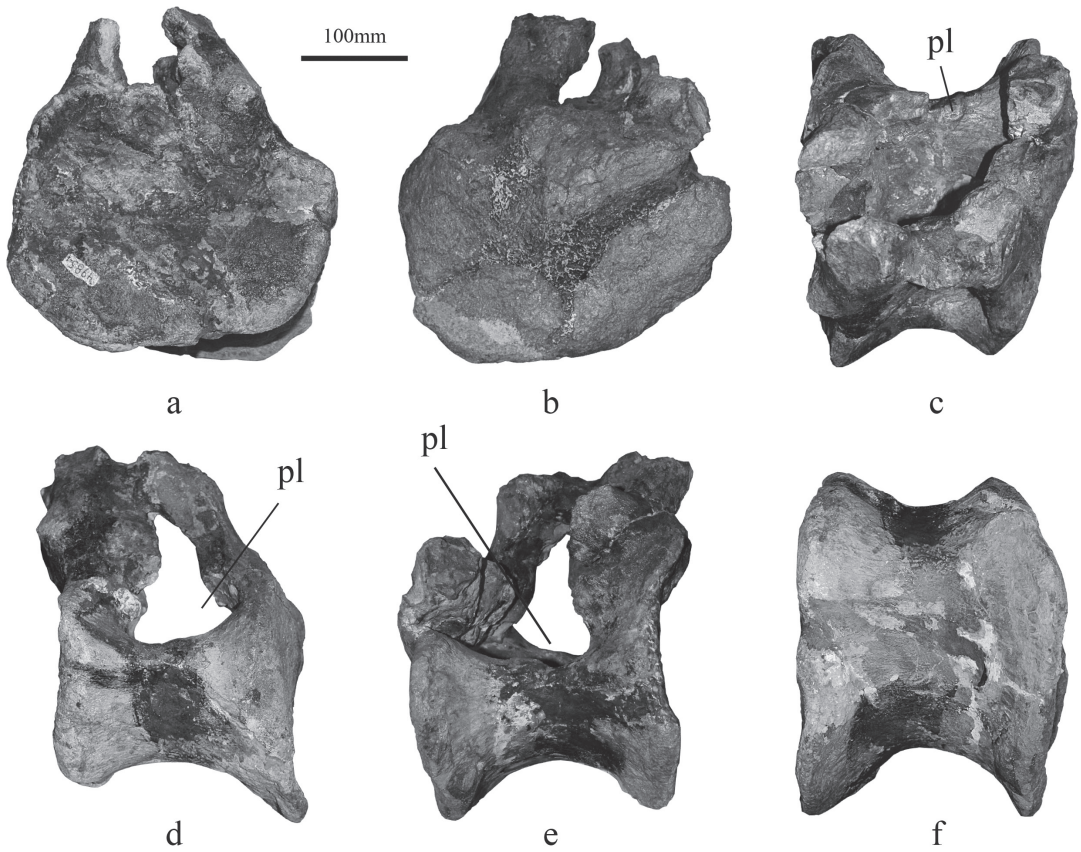

Figure 11.2. Middle-to-posterior dorsal vertebra of *L. atalaiensis* (MG 4805-1) in posterior (a), anterior (b), dorsal (c), right (d), left (e) and ventral (f) views.

Dorsal ribs: Several fragments of dorsal ribs are identified in the collections of Museu Geológico. They bear a solid bone tissue, albeit no proximal or distal fragment was found. The observed fragments probably correspond to middle-to-distal rib sections due the presence of lenticular to a slight L-shaped cross-section instead the well-developed L-shaped cross-section common in the proximal part of a dorsal rib. The fragments have a subcircular to slight mediolateral compressed outline, suggesting an anterior position in the dorsal series as occurs in *Giraffatitan* (1950). Lapparent and Zbyszewski (1957) referred the presence of flat fragments of dorsal ribs. A distal rib fragment is taphonomically associated with one of the preserved sacral neural spines, but it is not possible to allocate it along the dorsal rib series. The available information might suggests the presence of plank-like dorsal ribs (state 1 for the character #142 of Wilson, 2002). Nevertheless, we scored the character as unknown for *Lusotitan* due the absence of clear plank-like distal end for anterior dorsal ribs. These preserved dorsal ribs fragments do not show evidence

of pneumatization, but this feature is generally observed just in the proximal area of the dorsal ribs. Some fragments, with a more proximal position in the rib, show a pronounced lateral ridge, which probably gave rise to the capitulum.

Sacral vertebrae: One sacral centrum (MG 4801) is preserved lacking its neural arch as well as its posterior sector (Fig. 11.3). Lapparent and Zbyszewski (1957) interpreted this centrum as part of a cervical vertebra, assignation followed by Antunes and Mateus (2003). Mannion et al. (2013) interpreted this element as two adhered centra of a cervical and an anterior dorsal vertebrae. The anterior face is poorly preserved but seems to be convex with a slight concavity in the center. The lateral face is concave-to-flat anteroposteriorly and slopes medially resulting in a transverse short ventral face. This keel-structure is present in other sauropods such as *Tastavinsaurus* (Royo-Torres, 2009) or *Europasaurus* (Carballido and Sander, 2014; pers. observ, PM). The pleurocoels are anteriorly displaced and they are anteroposteriorly short. The pleurocoels are transversely deeper and the margins of pleurocoels are laterally stood out relatively to the lateral margin of the centrum. The right pleurocoel is deeper than the left one. In anterior view, the centrum bears a heart-shaped outline as occur in some *Europasaurus* sacral vertebra (pers. observ. PM) and in some material referred to "*Astrodon*" (Carpenter and Tidwell, 2005). Part of the ventral surface of the neural arch is preserved and bears a circular foramen.

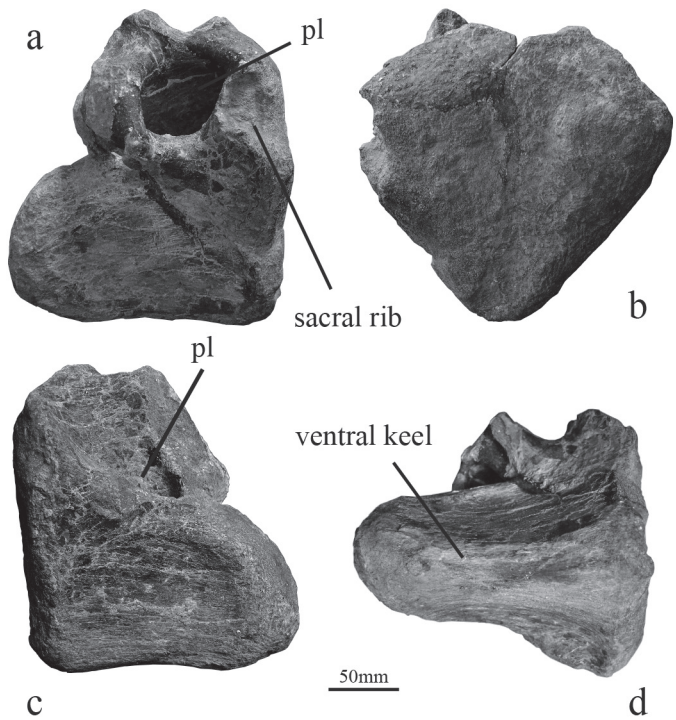

Figure 11.3. Incomplete sacral vertebra of *L. atalaiensis* (MG 4801) in right (a), anterior (b), left (c) and ventral (d) views.

Two not fused sacral neural spines are also preserved (Fig. 11.4). These neural spines were interpreted by Lapparent and Zbyszewski (1957) and Antunes and Mateus (2003) as dorsal neural spines. Mannion et al. (2013) described one of those neural spines interpreting as dorsal one or a possible sacral one. These neural spines are similar in several aspects, and one of them showing evidences of fusion (Fig. 11.4). The plate morphology of this spine with a marked transverse compression, evidences of fusion, a spdl not reaching the aliform process, and the comparison

of the present morphology with other sacral neural spines (Riggs, 1903; Janensch, 1950; Osborn and Mook, 1921; Canudo et al., 2008; Remes et al., 2009; Mocho et al., 2014) suggests that these two spines could be represent sacral neural spines. If these neural spines represent anterior sacral neural spines, they might bear a close morphology to the posterior dorsal neural spines of *Lusotitan*. In our phylogenetic analysis, we score characters related to the dorsal neural arch morphology as unknown.

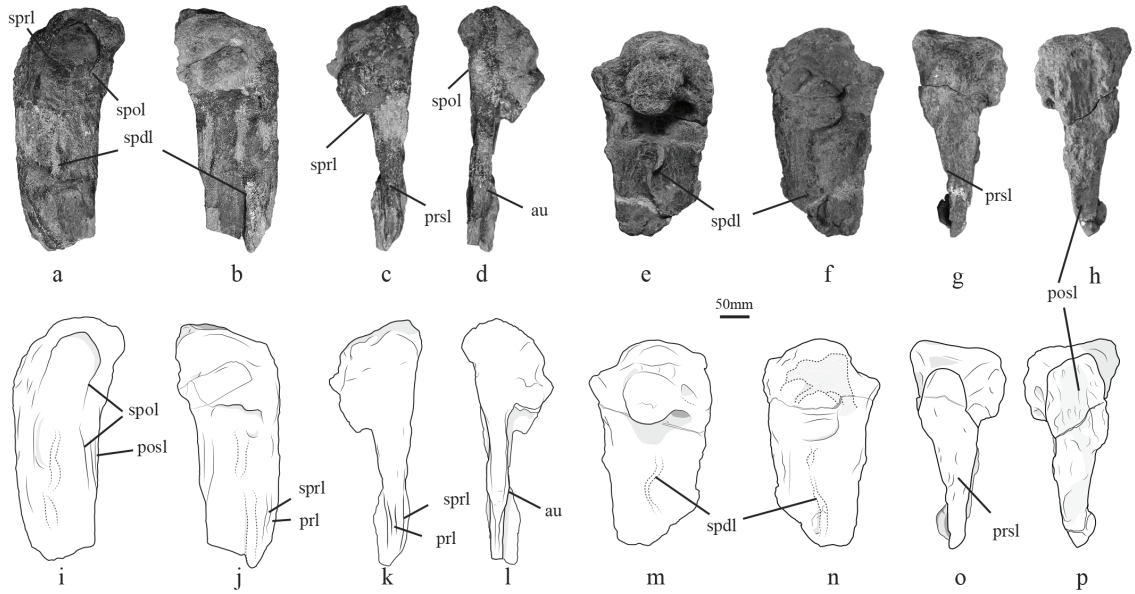

Figure 11.4. Sacral neural spines of *L. atalaiensis*. Unlabelled sacral spine in left (a), right (b), anterior (c) and posterior view; and respective schematic interpretations (i-l); MG 8807 in left (a), right (b), anterior (c) and posterior view and respective schematic interpretations (m-p). Fill in traced pinstripes: broken or eroded areas; traced line: broken borders.

These two elements interpreted as sacral neural spines have a tabular form that is compressed transversely and expanded distally in a triangular process. They are subrectangular in lateral view and the interpreted as the most anterior one have a posteriorly deflected distal tip (Fig. 11.4). The spinodiapophyseal laminae (spdl) have a sigmoid outline, but it is fractured in both spines. However, it is possible to verify that this lamina becomes dorsally shallow and ends below of the aliform process. It is interpreted that spdl is interrupted at midlength. In anterior view, the distal tip of the spine is expanded in a triangular process with a fan-shape morphology bearing a rounded-to-flat dorsal margin. The distal tip deflects to right side due some deformation. This expansion is more pronounced anteriorly and the ventral surface of this triangular process is dorsally excavated resulting in a deep fossa in both sides. The spol becomes pronounced at midheight near the triangular process. Dorsally, the spol diverges slight from the postspinal process. The most ventral sector of the spol on the most anterior sacral neural spine (MG 8807) is laterally projected, resulting in two ridges that are considered here as an autapomorphy of *Lusotitan atalaiensis*. The sprl also shows a pattern similar to the spol, more pronounced near the apex of the spine (diverging laterally from the prespinal process) and near the base of the spine. The most posterior sacral spine has an important development of the prespinal process denoting a trend of fusion between the sacral spines. The triangular aliform process is more anteroposteriorly restrict, besides the significant erosion, supported posteriorly by a stout lamina. In the lateral face of the most anterior spine there is a small fossa between the spdl and the dorsal sector of the sprl.

The only preserved sacral rib of *Lusotitan* was firstly identified as a right metacarpal II by Lapparent and Zbyszewski (1957). Antunes and Mateus (2003) reinterpreted this element as a sacral rib and was described in detail by Mannion et al. (2013).

Caudal vertebrae: Mannion et al. (2013) provided a detailed description for the caudal vertebrae (MG 4985 2-20) described as CdA-S. In this work we will add some new information in order to complete the descriptions proposed by these authors.

Along the preserved sequence could be identified at least two important gaps: between CdC (MG 4895-3) and CdD (MG 4895-4), and between CdE (MG 4895-5) and CdF (MG 4895-6) (Fig. 11.5). Between CdD (MG 4985-5) and CdE (MG 4985-6) there is a gap of approximately three vertebrae (Fig. 11.5). In addition to the impossibility of articulation between CdD and CdE, the morphology of the caudal ribs is particularly distinct.

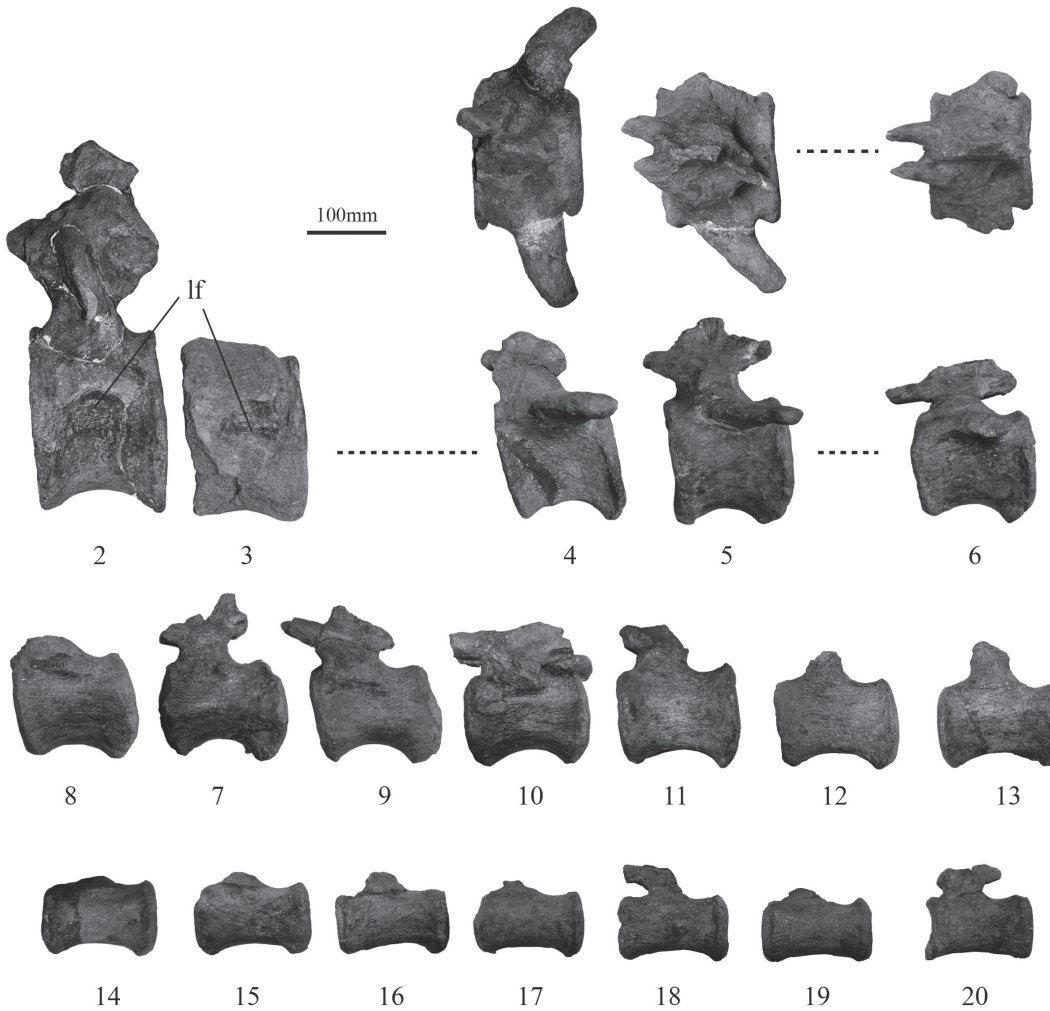

Figure 11.5. Preserved caudal series of *L. atalaiensis* in left view, except the top row, from MG 4805-2 and MG 4805-20. The number bellow to each vertebra made reference to the last label number. Top row: MG 4805-4, MG 4805-5 and MG 4805-6 in dorsal view. Traced line: probably gaps along the caudal series.

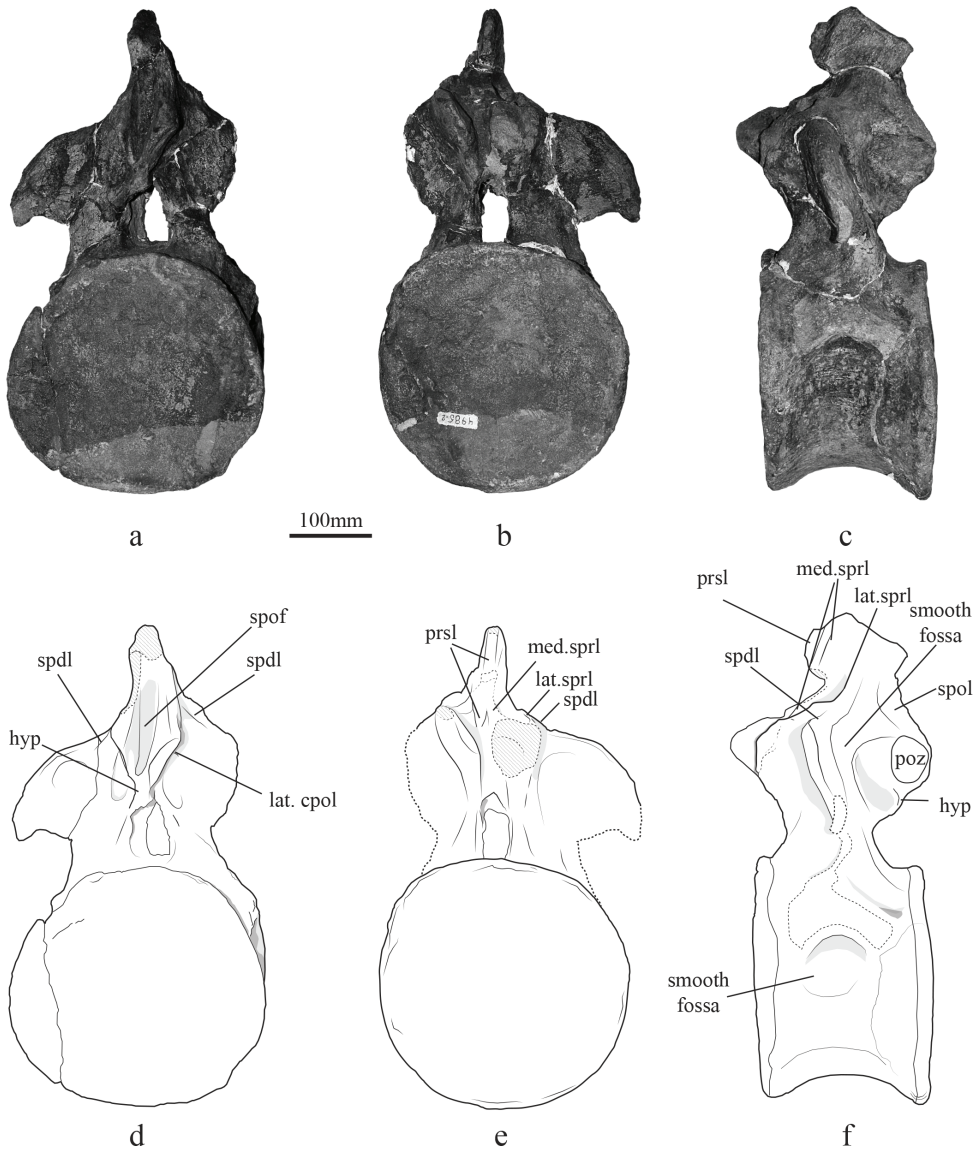

Figure 11.6. Proximalmost caudal vertebra of *L. atalaiensis* (MG 4805-2) in posterior (a), anterior (b) and left (c) views, and respective schematic interpretations (d, e, f). Fill in traced pinstripes: broken or eroded areas; traced line: broken borders.

CdA (MG 4985-2) corresponds to the most anterior centra of the caudal series. In CdA (MG 4985-2), Mannion et al. (2013) refer the presence of vascular foramina in the lateral face. Bellow the transverse processes, the lateral face of the centrum bears a smooth fossa which could be perforated or not by a small vascular foramina (not a pleurocoel). These smooth fossa plus foramina are also developed in the right side of CdB (MG 4985-3) and left side of CdC (MG 4985-4). From the prezygapophyses of CdA (MG 4985-2) up to the base of the neural spine parts two laminae, a medial sprl (med. sprl) which joins to the prespinal process, and a lateral sprl (lat. sprl) which develops posteriorly to the lateral surface of spine base (Fig. 11.6). Below postzygapophyses there are a small centropostzygapophyseal fossa (cpof) bordered by ridge-like hyposphene and a lateral centropostzygapophyseal lamina (lat. cpol), medial and laterally, respectively. In posterior

view, it is also possible to identify two fossae: *i*) a deep spinopostzygapophyseal fossa (spof; postspinal fossa of Mannion et al., 2013) on the posterior face of the neural spine that starts from the postzygapophyses and is bordered by the spol; and *ii*) a smooth fossa in the upper part of the posterior face of the caudal rib. Mannion et al. 2013 described the posterior face of the spine as rough, but the presence of sediment does not allow an accurate observation. CdA (MG 4985-2) bears a well-developed caudal rib fractured at the base. Mannion et al. (2013) refer the presence of two particular features on the caudal rib: *i*) a convex dorsal margin (considered by these authors as an autapomorphy of *Lusotitan*), and *ii*) the presence of a foramen on the ventral sector of the caudal rib. However, the ventral margin of the caudal rib is not preserved and the existence of this foramen cannot be tested.

The CdC (MG 4985-4) and CdD (MG 4985-5) are considered here as proximal caudal vertebrae. In both, the caudal ribs are long and posteriorly projected, surpassing the posterior articulation. On the other hand, in CdE (MG 4985-6) they are reduced disappearing in CdF (MG 4985-7) (Fig. 11.7). The MG 4985-7 have a more posterior position in the caudal series than MG 4985-8. The first caudal vertebra without caudal ribs is CdH (MG 4985-9, considered here as the first middle caudal vertebra). The comparison with other figured caudal series (e.g. Janensch, 1950; Osborn and Mook, 1921; Bonaparte et al., 2000) suggests that CdH (MG 4985-9) should a be a caudal vertebra located around the 15th position.

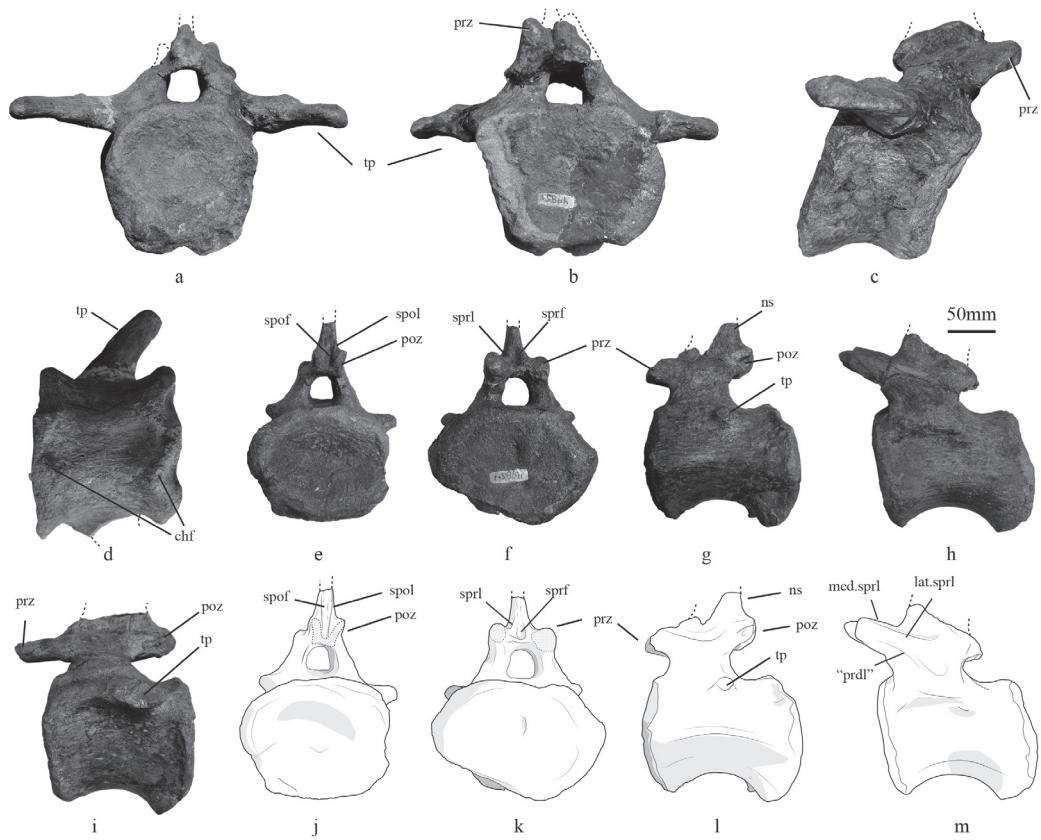

Figure 11.7. Anterior and middle caudal vertebrae of *L. atalaiensis*. MG 4805-4 in posterior (a), anterior (b) and right (c) views; MG 4805-5 in ventral view (d); MG 4805-7 in posterior (e), anterior (f) and left (g) views, and respective schematic interpretations (j, k, l); MG 4805-9 in left (h) view and its schematic interpretation (m) and MG 4805-6 in left (i) view; traced line: broken borders.

The dorsal surface of the prezygapophyses bears a small fossa interepreted as a sprl-f because is bordered by two laminae interpreted as the lat. sprl and med. sprl. This fossa progresses to the lateral face of the neural spines as occur in other sauropods such as *Europasaurus* (Carballido and Sander, 2014), the Areira Branca specimen (Yagüe et al., 2006) or *Spinophorosaurus* (pers. observ., PM). This fossa remains up to the most distal centra of *Lusotitan* preserving the base of the spine (MG 4985-18). In anterior view, the med. sprl borders a dorsoventral short sprf. In the sprf of the CdI (MG 4985-10) is possible to observe the presence of a prespinal lamina (prsl). The lat. cpol remains pronounced in these vertebrae and border laterally (with a med. cpol) a fossa, interpreted here as a centropostzygapophyses laminae-fossa. These fossae were interpreted by Mannion et al. (2013) as the region for the reception of the prezygapophyses distal tip.

MG 4985 11-20 corresponds to middle and posterior caudal vertebrae and are described in Mannion et al. (2013) (Fig. 11.8). Mannion et al. (2013) described the presence of elongated transverse pit in middle-to-posterior vertebrae and consider it as a diagnostic feature of *Lusotitan atalaiensis*. Transverse pits are also recognized in other middle and posterior caudal vertebrae such those of *Spinophorosaurus*, *Lapparentosaurus*, or *Cetiosaurus oxoniensis* (pers. observ., PM). These pits first appear in Cdf (MG 4985-7) as a circular pit in anterior and posterior faces. In CdM (MG 4985-14) these pits become transversely elongated, and between CdN (MG 4985-15) and CdP (MG 4985-17) these pits get a T-shaped form, particular unusual in sauropods, that is well-developed in the anterior face. The presence of T-shaped pits is considered as diagnostic of *Lusostitan*. Other particular feature appears from the CdM (MG 4985-14): a pair of smooth circular fossae in the ventral face of the centrum, anteriorly to the posterior chevron facets. These fossae are proposed as an autapomorphy of *Lusotitan atalaiensis*.

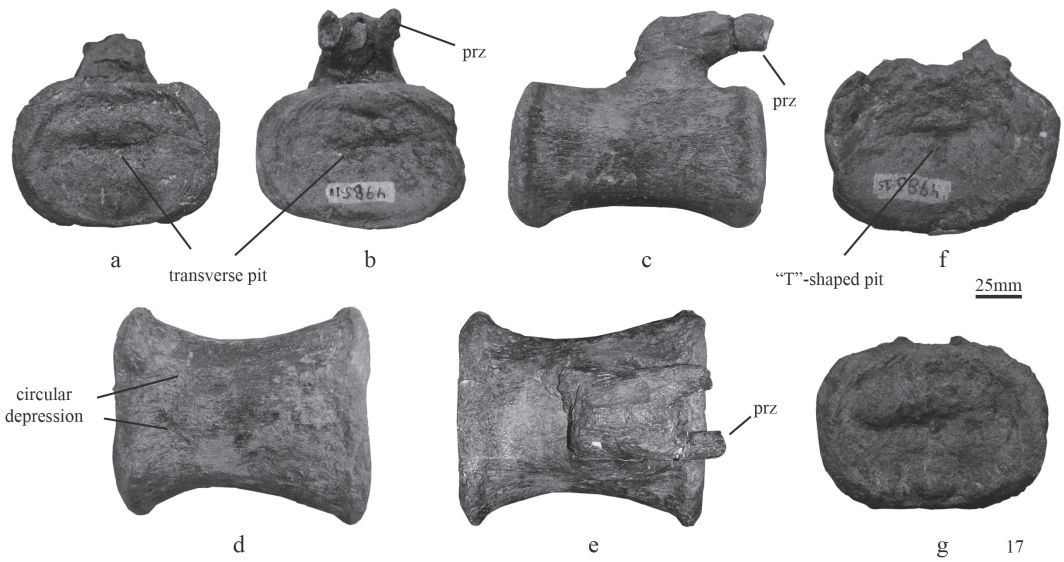

Figure 11.8. Middle-to-posterior caudal vertebrae of *L. atalaiensis*. MG 4805-18 in posterior (a), anterior (b), left (c), ventral (d) and dorsal (e) views. MG 4805-15 in anterior view (f) and MG 4805-17 in posterior view (g).

Chevrons: At least twelve chevrons belonging to the lectotype of *Lusotitan* are recognized. Mannion et al. (2013) described two of them, but several other proximal-to-distal chevrons were identified in the collections of the MG (Figs. 11.9, 11.10). Considering the existence of more complete sample, we provide a new description for the chevron series.

The proximal chevrons (MG 4810, an unlabeled chevron, MG 4806, and MG 4805) have a deep haemal channel (occupying approximately ½ of total length of chevron) (Fig. 11.9). The distal tip of the chevrons is distally deflected, which occurs below the point where haemal channel closes. No anterior and posterior processes are observed. The anterior and posterior margins become acute resulting in a keel. The dorsal rami are also transversely compressed with an anterior acute margin resulting crest-like structures. In the anterior chevrons with a more posterior position, the anterior crests of dorsal rami converge to the anterior keel located sagittally on the distal end. The anteriormost chevrons (fractured in the distal part) bear a well-defined dorsal bridge between the both circular heads. In posterior view, the bridge is arched with convexity directed ventrally. The distal end of the anteriormost chevrons does not bear the posterior keel present in anterior and middle chevrons. The anterior chevrons with a more posterior position are unbridged (MG 4806, MG 4805 and the unlabeled chevron) (Fig. 11.9). The articular facets of the chevrons are subcircular and compressed transversely and some (MG 4806) bears a posteromedial projection of the facets. In the case of bridged chevrons (MG 4810), the articulations are simple, but in the unbridged anterior chevrons, the articulations are composed by two facets: a dorsal facet and a posterior one slopping posteriorly (this remains to middle chevrons, e.g. MG 4808). The dorsal rami of the unbridged anterior chevrons are close to each other but never touch dorsally. Below haemal channel and between the anterior crests of the two dorsal rami there is a circular depression (unlabeled chevron, MG 4806).

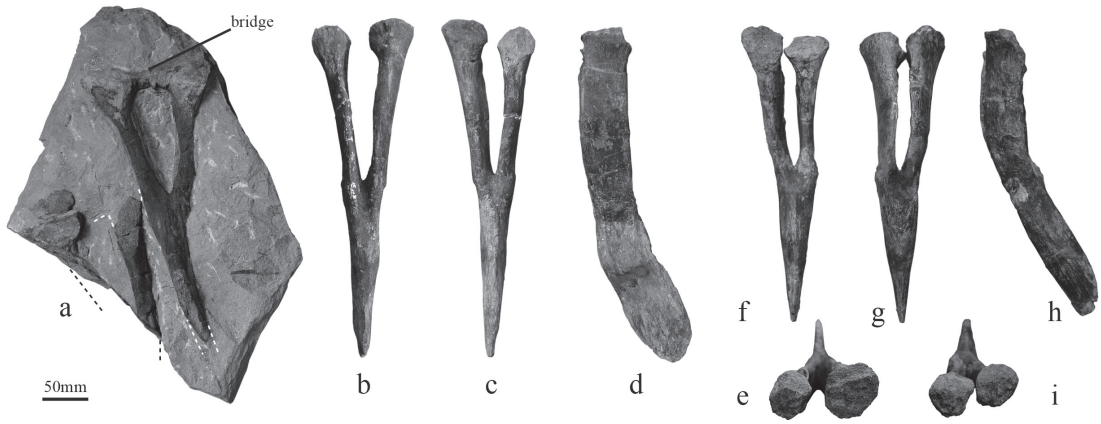

Figure 11.9. Anterior chevrons of *L. atalaiensis*. MG 4810 in posterior view (a); unlabelled anterior chevron in anterior (b), posterior (c), right (d) and proximal (e) views; MG 4806 in posterior (f), anterior (g), right (h) and proximal (i) views; traced line: broken borders.

In the middle (MG 4805, MG 4809) and posterior chevrons (MG 4807, MG 4808) the dorsal rami diverge laterally, and the posterior and anterior keel remains in the distal end (Fig. 11.10). The anterior margins of dorsal rami are also acute as well as in the anterior chevrons. This crest converge sagittally on the distal end. These chevrons are unbridged and the anterior circular depression is absent. In the middle chevrons (MG 4805), the chevron heads are anteroposteriorly compressed becoming transversely compressed in distal chevrons. In the middle chevrons, the articulations are composed by two facets, which is reduced to a single facet in the posterior ones. The haemal channel is deeper than the ½ of total chevron height, occupying almost the total length in distal ones. The distal end deflects posteriorly, and never develops anterior or posterior processes as in diplodocids (e.g. Hatcher, 1901). The preserved distal chevrons do not acquire a ventral slit.

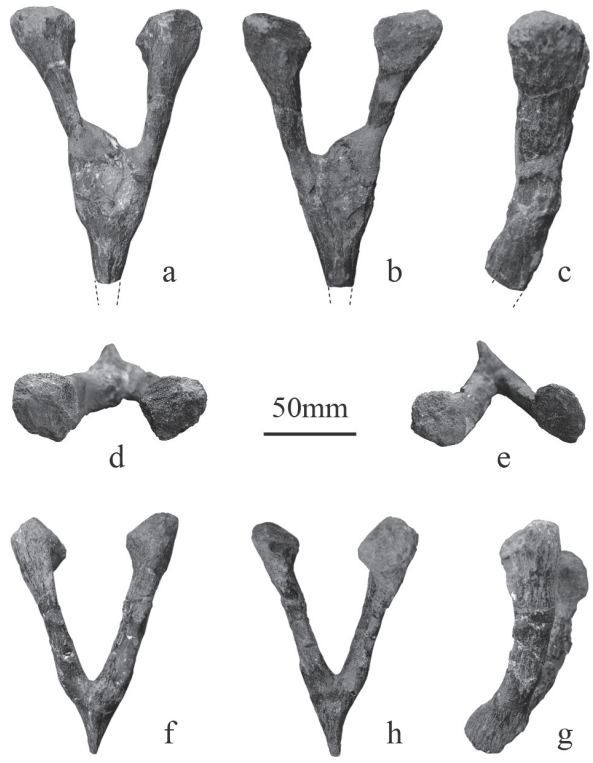

Figure 11.10. Middle and posterior chevrons of *L. atalaiensis*. MG 4809 in anterior (a), posterior (b), left (c) and proximal (d) views; and MG 4808 in proximal (e), anterior (f), posterior (g) and left (h) views; traced line: broken borders.

Right and left humerus: The proximal sections of right and left humeri are preserved (Fig. 11.11). Mannion et al. (2013) only describe the right humerus of *Lusotitan* lectotype. As was referred by these authors, the deltopectoral crest is anteriorly directed, pronounced, and rounded with rough surface and subrectangular outline in cross-section. This crest is slight and medially displaced relatively to the lateral margin of the humerus, and is constricted dorsoventrally (located in the most ventral region of humeral proximal end). The lateral face of the deltopectoral crest is transversely concave. The anterior surface of the proximal section is concave, as referred by Mannion et al. (2013), and bears a located suboval concavity below the humeral head as in other sauropods such as *Lourinhasaurus* (Mocho et al., 2014). The proximal end of the left humerus was located in the Museu Geológico collections and bears the same general morphology than the left one. Although the weak state of preservation (erosion, cracks and some reconstruction), the transition between the dorsal and lateral edge of the humerus bears a rounded prominence, not present in the right humerus.

Left ulna: As referred Lapparent and Zbyszewski (1957), a section of the left ulna was preserved. Mannion et al. (2013) interpreted it as a right ulna. After the direct observation of this element, we decided to follow the interpretation of Lapparent and Zbyszewski (1957). The proximal end of the ulna lacks the extremity of the ulnar anteromedial process (Fig. 11.12). The proximal surface of the lateral process slopes laterally, bearing a slight concavity resulting in slight hook-shaped profile in anterior view. The midpoint of proximal surface is elevated (olecranon *sensu* Mannion et al., 2013) not as in some titanosaurs (e.g. Poropat et al., 2015). Anteriorly and posteriorly to this convexity, there are two circular concavities. In

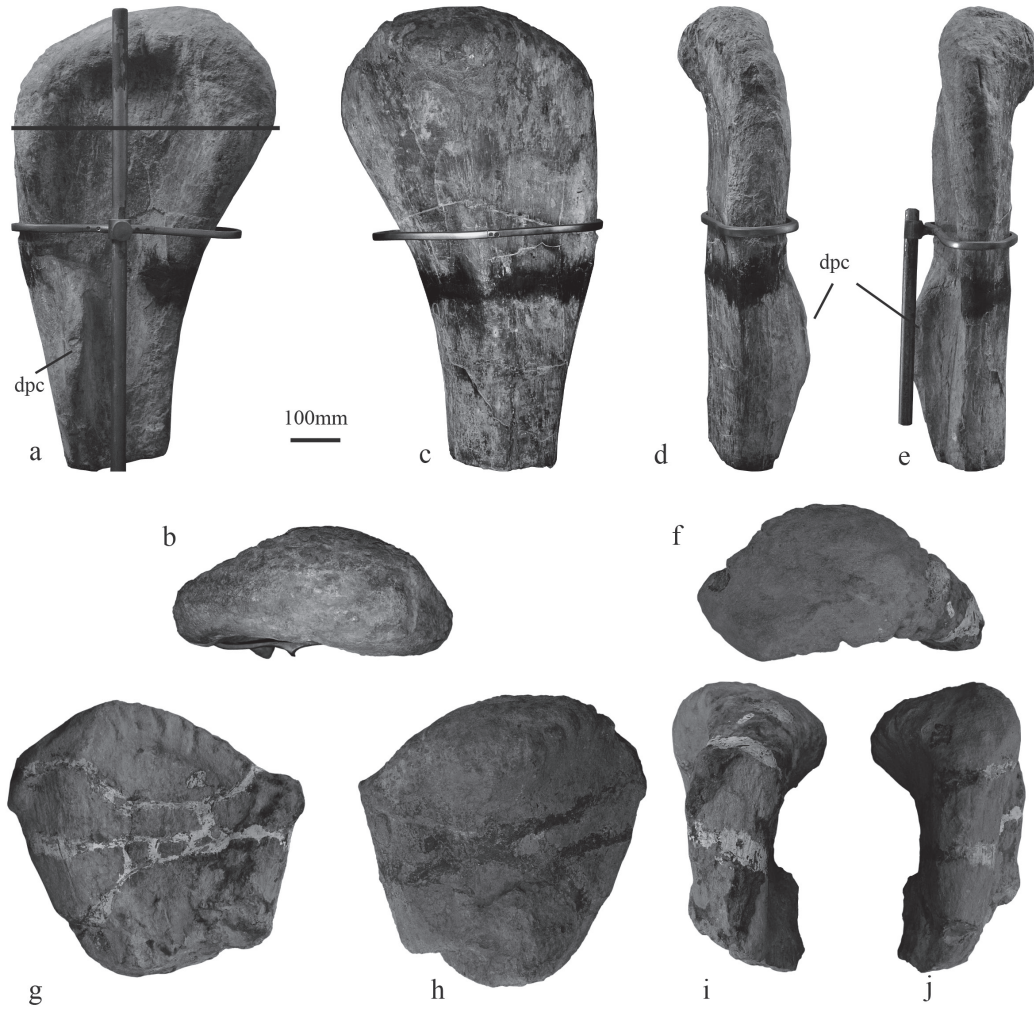

Figure 11.11. Humeri of *L. atalaiensis*. Right humerus (MG 4964) in anterior (a), dorsal (b), posterior (c), lateral (d) and medial (e) views and left humerus (MG 4944) in dorsal (f), anterior (g), posterior (h), lateral (i) and medial (j) views.

proximal view, the ulna bears a triradiate outline, with a strong anterior concavity (corresponds to the area for the articulation with the radius) and slight concave posterolateral and medial edges. The posterolateral and medial surfaces of the proximal end are slightly concave. The angle between the two processes is less than 90º. Besides the incompleteness of the anteromedial process, this process is thicker and probably longer than the anterolateral one.

Right and left radii: A complete left radius and a distal section of the right one are preserved (Fig. 11.13). This element is described by Mannion et al. (2013) but some information could be incorporated. The radius is higher than tibia (ratio radius/tibia length=1,3), and the element is anteroposteriolly compressed along its proximodistal width. The posterior face of the radius bears a circular depression bellow the lateral projection of proximal surface. The proximal section has a concave and rough surface. The distal section of the right radius is not so compressed anteroposteriorly than the left one and has a more subsquared outline in distal view.

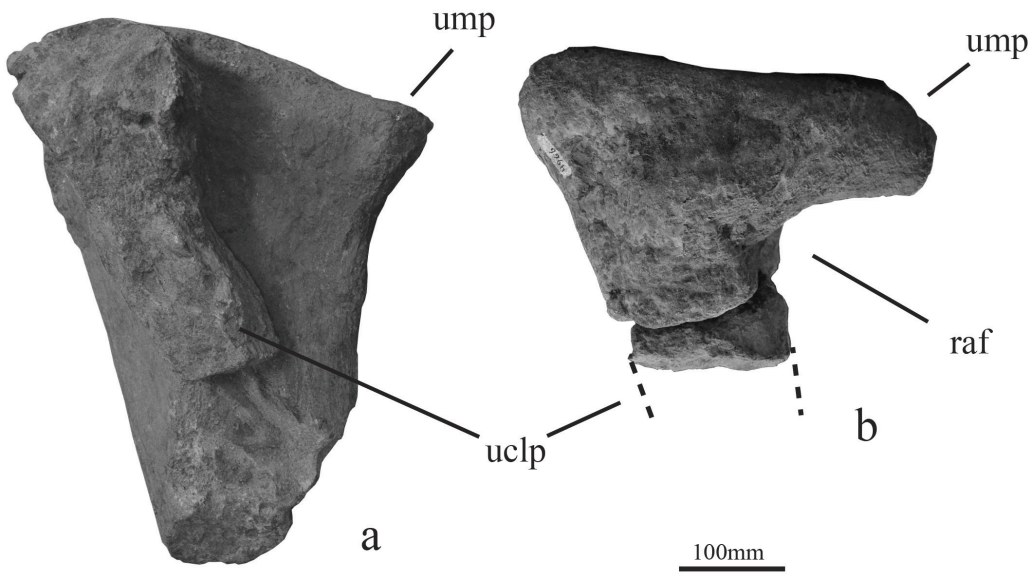

Figure 11.12. Left ulna of *L. atalaiensis* (MG 4966) in anterior (a) and dorsal (b) views. Traced line: broken borders.

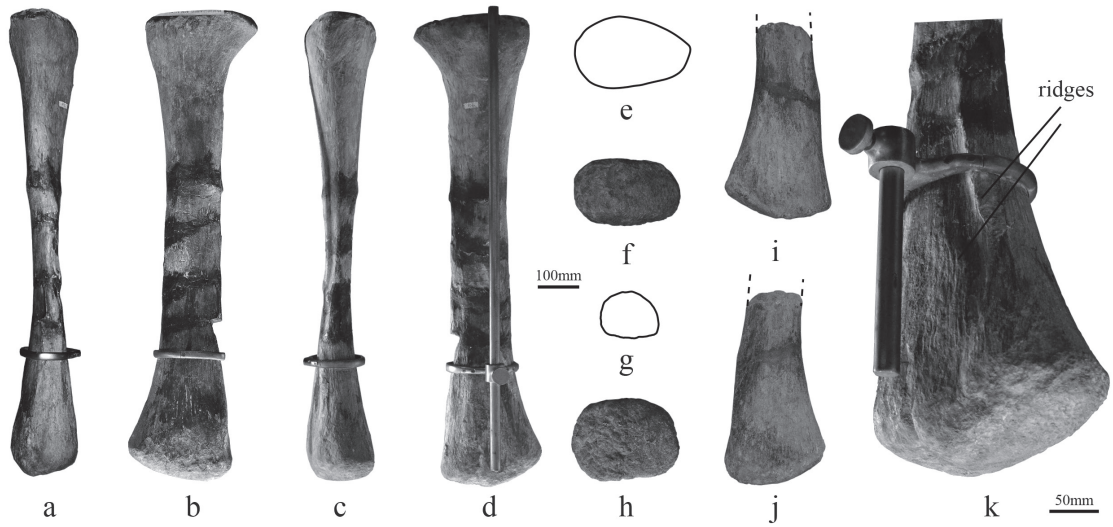

Figure 11.13. Radii of *L. atalaiensis*. Left radius (MG 4960) in lateral (a), anterior (b), medial (c), posterior (d) and proximal (e) views and the outline of distal end (f) views; right radius (MG 4958) in distal (h), posterior (i) and anterior (j) views and diaphysis cross-section outline (g). A close up in medioposterior view of the left radius posterior surface (k). Traced line: broken borders.

Left ischium: Mannion et al. (2013) described this element based on Lapparent and Zbyszewski (1957) and Antunes and Mateus (2003) figuration. We have located this bone in Museu Geológico and the assessment of the left ischium (MG 4952) made necessary a revised description of this element (Fig. 11.14). The acetabulum is transversely concave and in is not particularly individualized. This surface transits continuously to the lateral surface of the ischium. The medial face of proximal plate is smoothly concave. The pubic peduncle has a convex outline in lateral

view. In anterior view, the pubic articulation bears a subrectangular outline but with a slight constriction in middle, an exclusive feature of *Lusotitan*. The ischiatic peduncle has a tabular morphology (resulting in a compressed elliptical cross-section) with the dorsal edge thicker and rounder than the ventral one. The ventral margin of the ischiatic blade shows an emargination for the pubic peduncle. The iliac peduncle has a rough and flat surface being suboval in dorsal view and more constricted near the acetabulum. In the lateral face, at the base of the ischiatic peduncle near its posterior edge there is a tuberosity not bordered by a groove as in *Lourinhasaurus* (Mocho et al., 2014). The anteroposterior width of the pubic peduncle is shorter than its proximodistal width. The ischiatic blade twists distally. Nevertheless, the absence of its distal end, do not allow testing the presence of coplanar ischiatic peduncles.

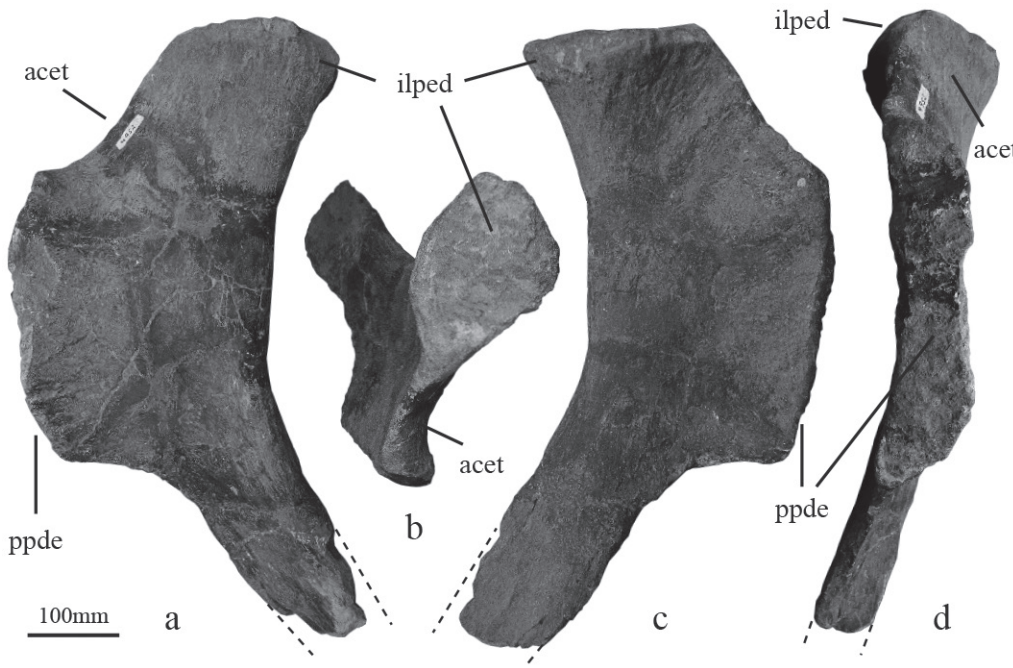

Figure 11.14. Left ischium (MG 4952) of *L. atalaiensis* in lateral (a), proximal (b), medial (c) and anterior (d) views. Traced line: broken borders.

Left pubis: The preserved pubis was described and figured initially by Lapparent and Zbyszewski (1957) and figured by Antunes and Mateus (2003) and Mannion et al. (2013). However we consider that the pubis can be not correctly orientated in the last two works and so, the supposed lateral face in interpreted here as the medial face, and the ischiatic peduncle is interpreted as the iliac peduncle and acetabulum. Considering this, we provide a new description and figuration for this element (Fig.11.15). The pubis is mediolaterally compressed, with an anteriorly projected pubic peduncle. The anterior margin of the distal pubic peduncle has a rounded projection, considered diagnostic of *Lusotitan atalaiensis*. The ischiatic and the pubic peduncle lie in the same plane. In the medial face of the proximal plate is possible to observe a closed obturator foramen (compressed dorsoventrally). It is not visible in the lateral face because this part of the pubis is reconstructed. The medial face of the ischiatic peduncle is slightly concave near the distal tip of the ischiatic articulation. The posterior border of the pubic peduncle bears a very soft S profile in posterior view. The pubic symphysis is restricted to the posterior distal tip of the pubic peduncle and corresponds to a triangular facet. The pubic blade expands distally and becomes transversely thicker. In distal view, the distal end has an elliptical outline mediolaterally compressed. The

distal surface is rough and flat-to-concave. The lateral and medial face of the pubic peduncle is convex transversely. The ischiatic articulation bears a lenticular outline in posterior view and its proximodistal width is less than 1/3 of pubic total length. The iliac peduncle is low (not detached from the acetabulum) and has a lenticular outline in dorsal view. The acetabulum surface is not a marked surface and transits smoothly to the lateral face of the proximal plate. The surface bears a circular process in center that that no seems to be pathological.

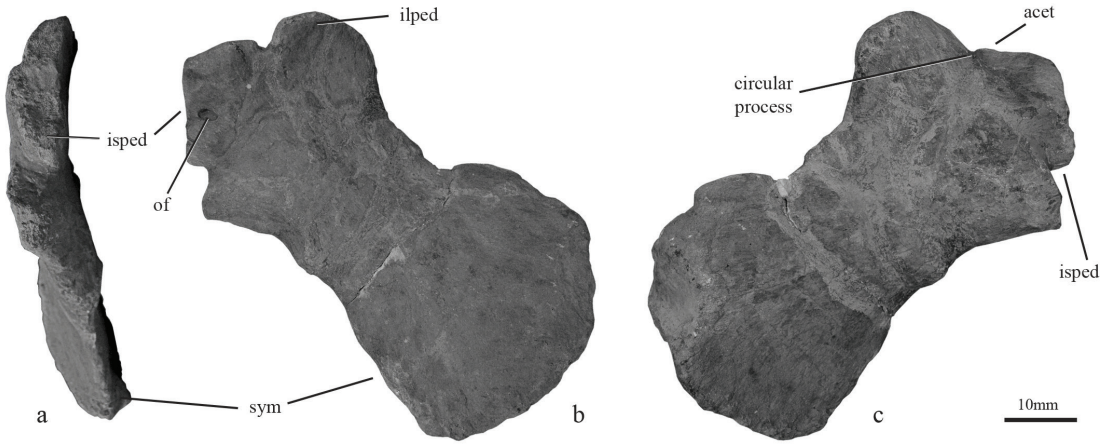

Figure 11.15. Left pubis (MG 4965) of *L. atalaiensis* in posterior (a), medial (b) and lateral (c) views.

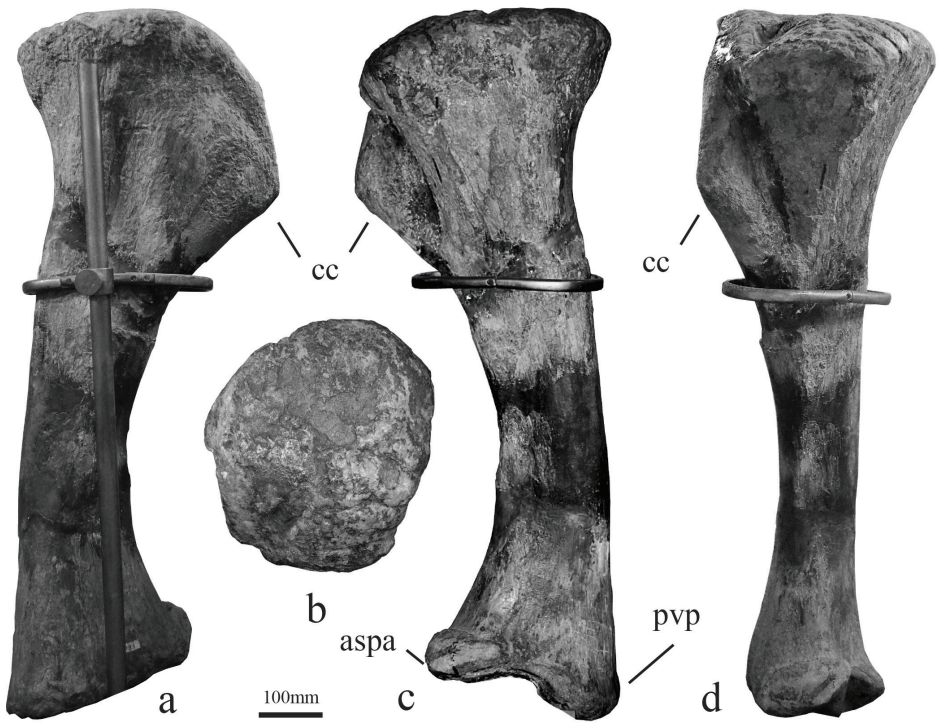

Figure 11.16. Left tibia (MG 4981) of *L. atalaiensis* in anterior (a), proximal (b), posterior (c) and lateral (d) views.

Left tibia: A detailed description for the left tibia (Fig. 11.16, MG 4981) is provided by Mannion et al. (2013). As these authors referred the marked curvature of the tibia is also considered here as an autapomorphy of *Lusotitan* (with convexity directed medially). The cnemial crest is pronounced, bears a triangular format in posterior view, and has a ventrolaterally directed apex, also considered as autapomorphy of *Lusotitan*. The cnemial crest is asymmetric and has a rough dorsal edge longer than the ventral one. The cross-section of tibial shaft bears a lacrimal outline, with lateral acute margin producing a dorsoventral crest bordered by smooth grooves. The cnemial crests and the triangular articular surface for the fibula meets in this crest, tentatively assigned as autapomorphy of *Lusotitan atalaiensis*. The posteroventral process and the articular surface for the ascending process of the astragalus are distally separated by a well-marked concavity. Nevertheless, as referred Mannion et al. (2013), the absence of a groove in the posterior surface of the distal end separating the posteroventral process and the articular surface for the ascending process of astragalus could be considered autapomorphic of *Lusotitan*. The articular surface for ascending process is considerably developed and its dorsal margin is almost horizontal and transits to the lateral face of the tibial shaft by a break of slope, producing a step-like structure, also diagnostic for *Lusotitan atalaiensis*.

Left fibula: Only the proximal end of the left fibula is preserved (Fig. 11.17, MG 4982). The reassessment of this element allows us to provide a new detailed description. The medial surface of the fibular proximal end is markedly concave for the reception of the tibia, resulting in an arched profile in proximal view. The articular surface for the tibia does not bear a marked triangular facet. This facet is dorsoventrally restricted. In medial view, the dorsal margin is straight. The proximal surface is rough and flat. On the anterior face of the fibula there is a crest-like anterior trochanter with the apex located near to the proximal surface of the fibula. Besides this morphology, the crest-like anterior trochanter is not so well developed as in somphospondylians (D'Emic, 2012). The lateral surface of the fibular proximal end is anteroposteriorly convex. The most distal part preserves in the lateral face a slight and rough bulge interpreted as the lateral trochanter. The preserved sector of the fibular diaphysis has an elliptical outline mediolaterally compressed.

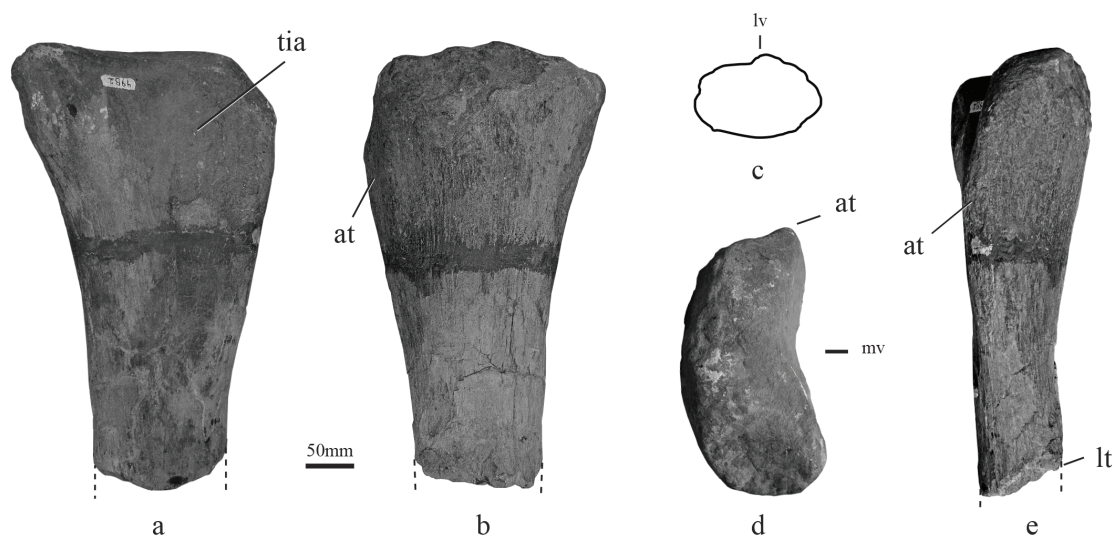

Figure 11.17. Left fibula (MG 4982) of *L. atalaiensis* in medial (a), lateral (b), proximal (d) and anterior (e) views, and the cross section outline of the fibula diaphysis (c).

Left astragalus: Mannion et al. (2013) provided a detailed description for MG 4803. The ascending process of astragalus does not reach the posterior margin of the astragalus but surpass the anterior 2/3 of astragalus. The posterior face of ascending process is pierced by several smooth foramina (Fig. 11.18).

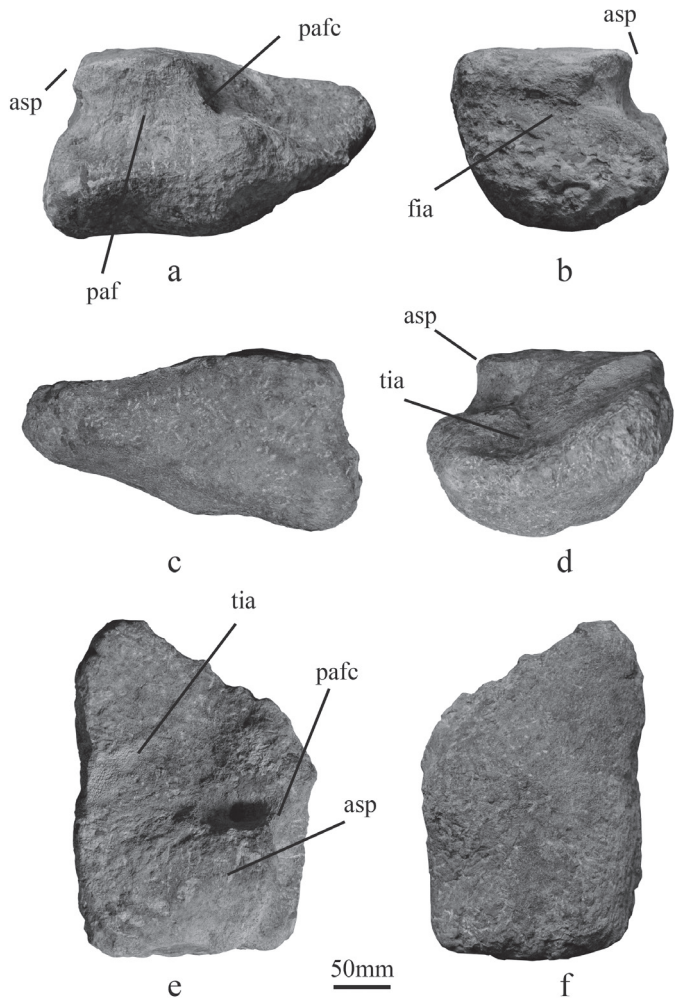

Figure 11.18. Left astragalus (MG 4803) of *L. atalaiensis* in posterior (a), medial (b), anterior (c), lateral (d), proximal (e) and distal (f) views.

11.6. PHYLOGENY

In order to obtain an accurate phylogenetic approach for *Lusotitan atalaiensis* we used the updated version of Wilson (2002) and Upchurch et al. (2004) data matrices proposed by Mocho et al. (2014), including the codification for *Brachiosaurus altithorax* proposed by Royo-Torres et al. (2014). For a more precise phylogenetic position of *Lusotitan* within Titanosauriformes we also used the D'Emic (2012) data matrix, introducing some changes in *Tastavinsaurus sanzi* based on personal observations of the holotype and referred material (Canudo et al., 2008; Royo-Torres, 2009; Royo-Torres et al., 2012). Based in Royo-Torres et al. (2014) and personal observations, we also provide some modifications to *Cedarosaurus*, *Venenosaurus* and *Turiasaurus*. All

data matrices were analyzed using TNT 1.1 (Goloboff et al. 2003) in order to find the most parsimonious trees (MPTs). It is used a heuristic tree search performing 1000 replicates of Wagner trees (using random addition sequences) followed by tree bisection reconnection (TBR) as swapping algorithm, saving 100 trees per replicate. All changes proposed in this study to the published data matrices are detailed in a supplementary information file. To test the robustness of the phylogenetic hypotheses, Bremer support and bootstrap (absolute frequencies based on 5000 replicates) values were also obtained with TNT 1.1. (Goloboff et al., 2003).

11.6.1. Results

Analysis I. Wilson (2002) data matrix. As in the analysis carried out by Wilson (2002), the multistate characters 8, 37, 64, 66 and 198 were considered ordered. The result of this analysis is 57 MPTs of 517 steps with a consistency index (CI) of 0.552 and a retention index (RI) of 0.751 (Fig. 11.19). The strict consensus for the 57 MPTs produces a polytomy between *Jobaria*, *Haplocanthosaurus*, Diplodocoidea and Macronaria. *Lusotitan* is recovered in a polytomy at the base of Macronaria with *Brachiosaurus*, *Lourinhasaurus*, *Tehuelchesaurus*, *Camarasaurus*, *Giraffatitan*, *Tastavinsaurus*, *Cedarosaurus*, *Venenosaurus*, *Phuwiangosaurus*, *Euhelopus* and Lithostrotia. An exploratory majority rule (50%) recovers *Lusotitan* as a basal Titanosauriform in a polytomy with Laurasiformes, Brachiosauridae and Somphospndyli. Using the pruned trees function in order to identify "wild-card" taxa, it is possible to identified two nodes with the removal of *Tehuelchesaurus*, and one node with the removal of *Lusotitan*, *Phuwiangosaurus* and *Patagosaurus*. Carrying out an analyses without *Tehuelchesaurus*, it is recovered 18 MPTs of 508 steps with a consistency index (CI) of 0.563 and a retention index (RI) of 0.762. The strict consensus results in a tree with Titanosauriformes and *Lusotitan* as a basal titanosauriform in polytomy with *Brachiosaurus*, *Giraffatitan*, Laurasiformes and Somphospondyli.

In the first analyses, *Lusotitan atalaiensis* is considered as member of Macronaria by the presence of opisthocoelous posterior dorsal vertebrae (character #105), absence of forked chevrons (character #143) and haemal channel approximately 50% of the chevron depth (character #146). Without *Tehuelchesaurus*, the inclusion of *Lusotitan* within Titanosauriformes is supported by the absence of forked chevrons (character #143) and haemal channel approximately 50% chevron depth (character #146).

Analysis II. Upchurch et al. (2004) data matrix. As in the analysis carried out by Upchurch et al. (2004), *Marasuchus* is considered as outgroup and are omitted a priori the following taxa: *Aragosaurus*, *Andesaurus*, *Argentinosaurus*, *Lapparentosaurus*, *Nigersaurus*, *Paluxysaurus* (="*Pleurocoelus-tex*"). It is also incorporated a fix topology at the base of cladogram applied in the same study. This analysis yielded 18 MPTs with 683 steps and CI=0,469 and RI=0,779 (Fig. 11.20). The strict consensus follows the main topology obtained in recent publications (Wilson and Upchurch, 2009; Royo-Torres et al., 2012; Royo-Torres and Upchurch, 2012; Mocho et al., 2014) recovering Camarasauridae as a monophyletic clade and composed by *Camarasaurus*, *Lourinhasaurus* and *Tehuelchesaurus*. *Lusotitan* is placed within the Titanosauriformes, in particular, within Brachiosauridae, with *Brachiosaurus*, *Giraffatitan*, *Tastavinsaurus* and *Cedarosaurus*. *Lusotitan* appears as the sister taxon of *Tastavinsaurus* + *Cedarosaurus*.

The hypothesis obtained from Upchurch et al. (2004) data matrix includes *Lusotitan* within Titanosauriformes by the presence of: *i*) dorsal centra dorsoventrally compressed (character #131); *ii*) neural arches of middle caudal vertebrae displaced anteriorly from the midpoint of respective centra (character #185). *Lusotitan* is considered as a member of Brachiosauridae by the presence of two of the five synapomorphies of the group (the other three are not available): *i*) middle caudals dorsoventrally compressed (character #184); and *ii*) pronounced deltopectoral crest (character #219). Some of these characters are not codified by Wilson (2002), which could

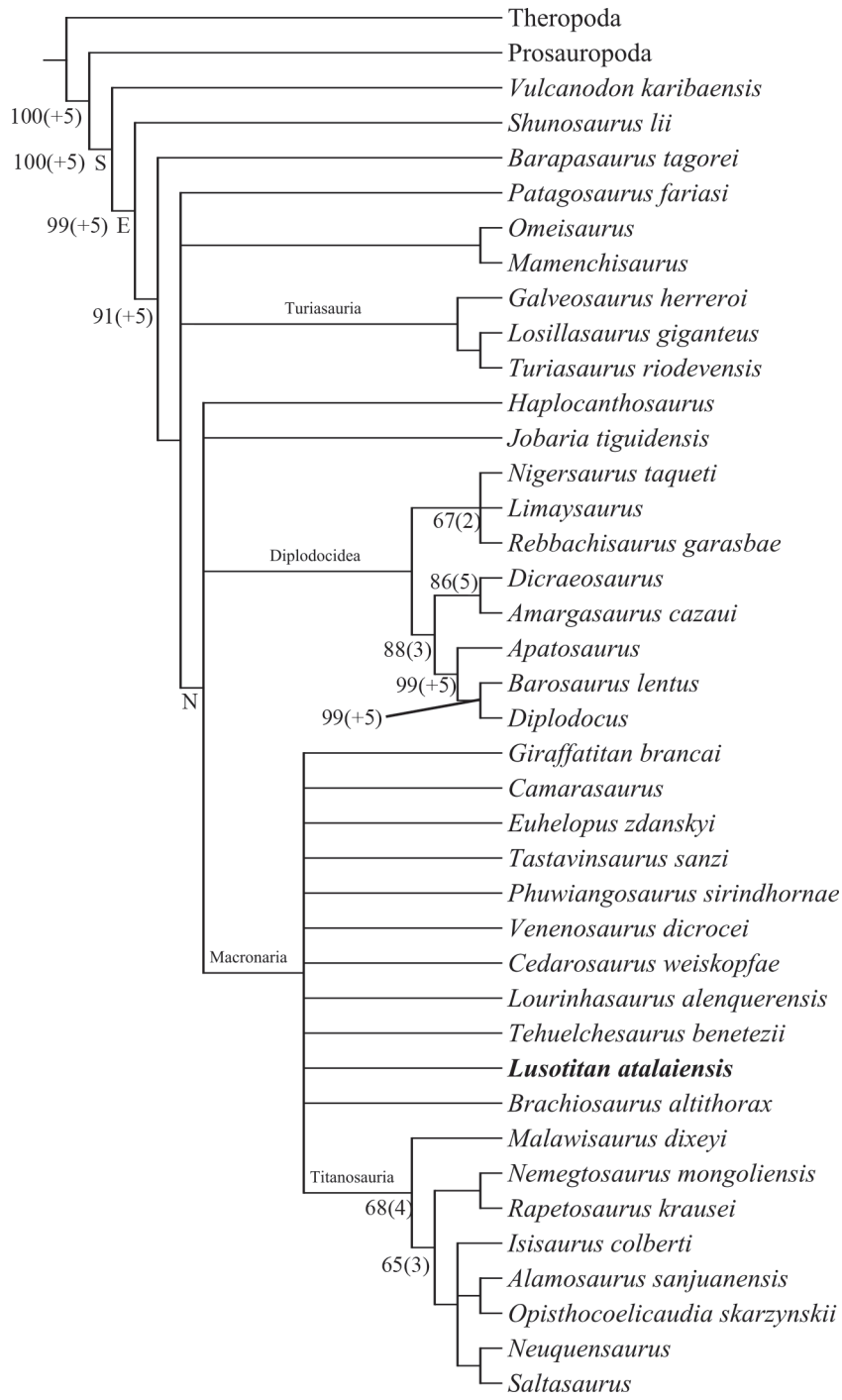

Figure 11.19. Strict consensus of 57 MPTs of 517 steps with a consistency index (CI) of 0.552 and a retention index (RI) of 0.731 obtained from Wilson (2002) data matrix. S – Sauropoda, E – Eusauropoda, N – Neosauropoda, M – Macronaria, C – Camarasauromorpha, T – Titanosauriformes, So – Somphospondyli, Ti – Titanosauria, L – Lithostrotia. Number in the nodes indicates the bootstrap values and (with asterisk) the Bremer support values.

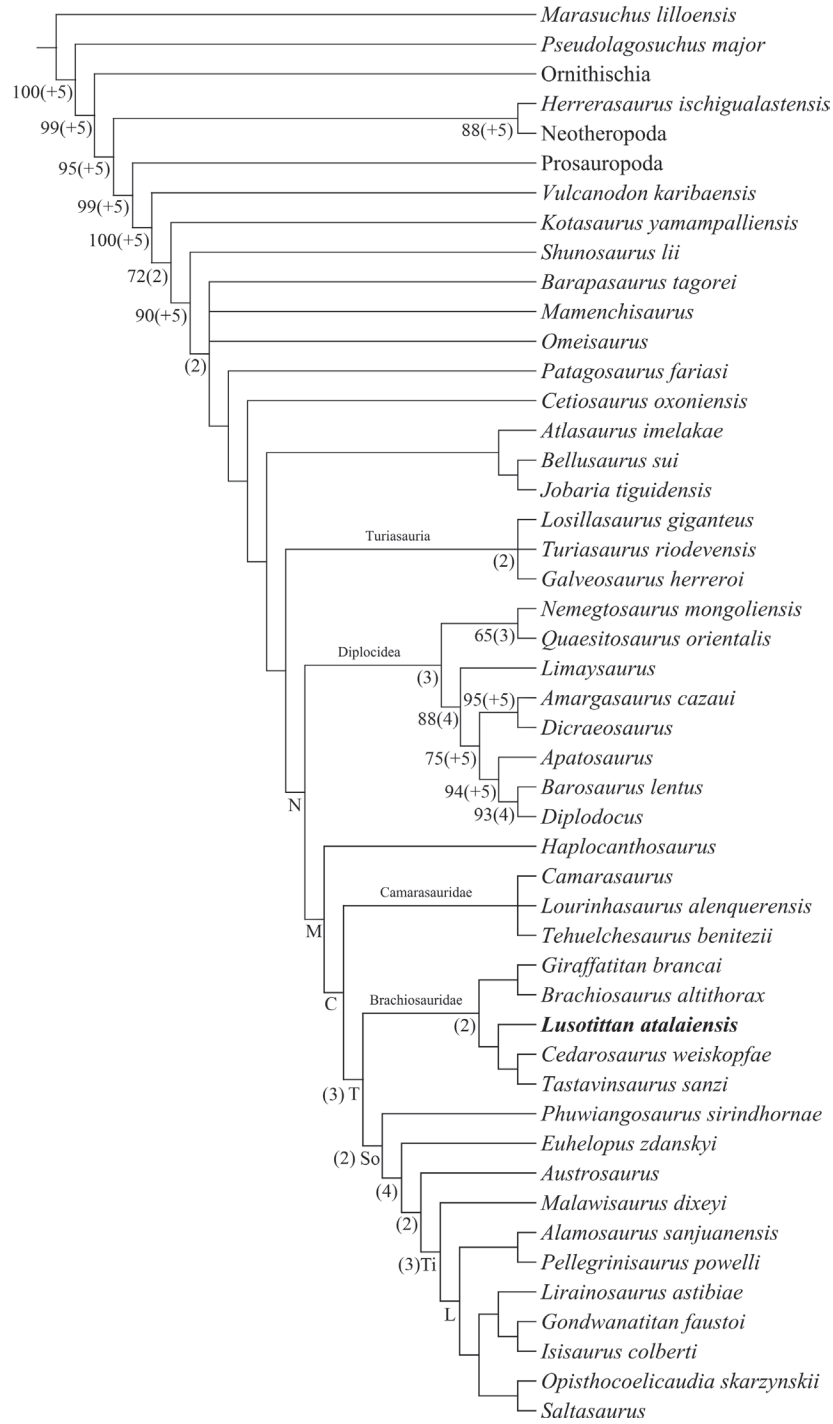

Figure 11.20. Strict consensus of 18 MPTs of 683 steps with a consistency index (CI) of 0.469 and a retention index (RI) of 0.779 obtained from Upchurch et al. (2004) data matrix. S – Sauropoda, E – Eusauropoda, N – Neosauropoda, M – Macronaria, C – Camarasauromorpha, T – Titanosauriformes, So – Somphospondyli, Ti – Titanosauria, L – Lithostrotia. Number in the nodes indicates the bootstrap values and (with asterisk) the Bremer support values.

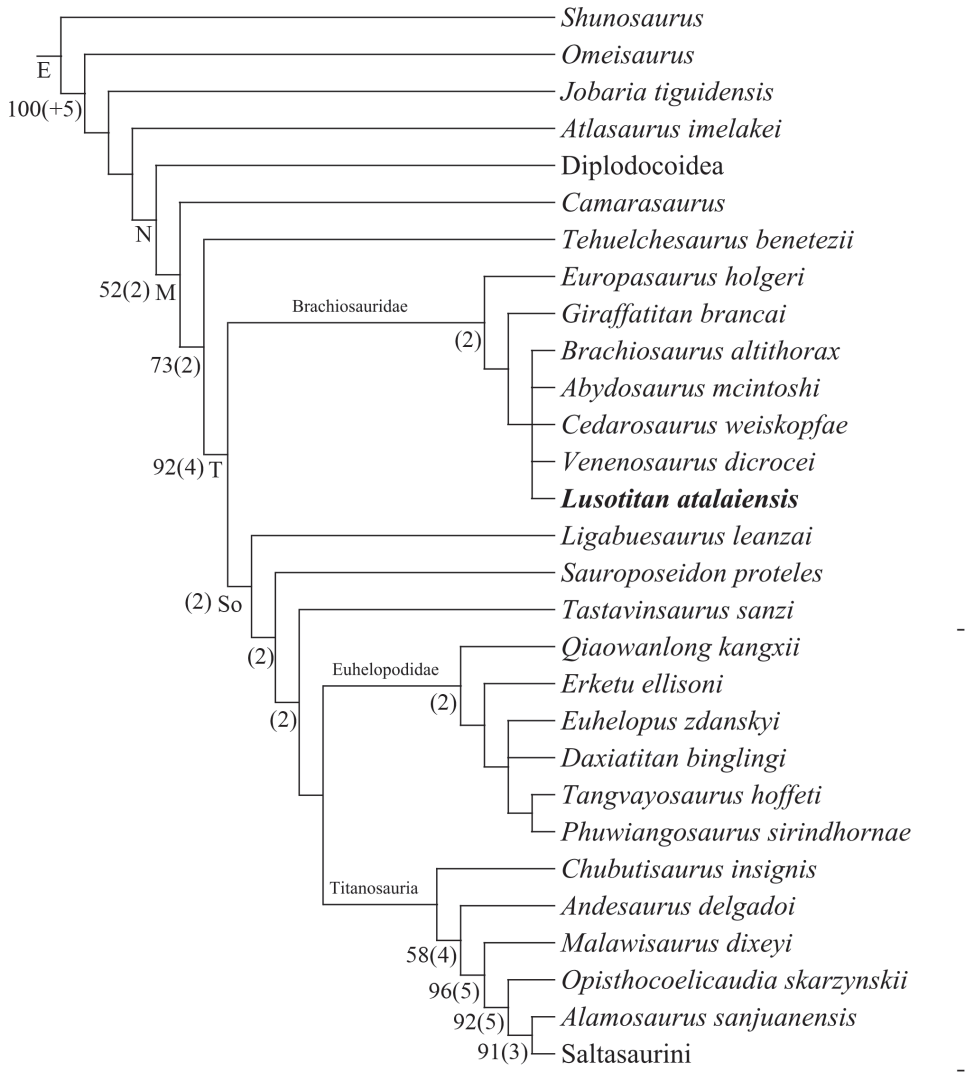

Figure 11.21. Strict consensus of 3 MPTs of 206 steps with a consistency index (CI) of 0.607 and a retention index (RI) of 0.801 obtained from D'Emic (2012) data matrix. S – Sauropoda, E – Eusauropoda, N – Neosauropoda, M – Macronaria, C – Camarasauromorpha, T – Titanosauriformes, So – Somphospondyli, Ti – Titanosauria, L – Lithostrotia. Number in the nodes indicates the bootstrap values and (with asterisk) the Bremer support values.

explain the difficulty to achieve the position of *Lusotitan* within Brachiosauridae. This phylogenetic hypothesis identified as an exclusive feature of *Lusotitan* the ratio of centrum length:height for the proximal caudals > 0,6 (character #177).

Analysis III. D'Emic (2012). As in the analysis carried out in D'Emic (2012), the eusauropod *Shunosaurus lii* is considered as outgroup and the multistate characters 8, 37, 64, 66 and 198 were considered ordered. This analysis yielded 3 MPTs with 206 steps and CI=0,607 and RI=801 (Fig. 11.21). The strict consensus follows the main topology obtained in D'Emic (2012) and includes *Lusotitan* in Titanosauriformes and as member of Brachiosauridae, in a clade more derived than *Giraffatitan*, which also includes, in a polytomy, *Brachiosaurus*, *Venenosaurus*, *Abydosaurus* and

Cedarosaurus. The assignation of *Lusotitan* to Titanosauriformes is supported by the following synapomorphies: *i*) anterior process of the ulna longer and more robust than the medial one (character #85); *ii*) pubis length relative to puboischiatic contact less than or equal to 2,5 (character #101) and *iii*) the ischium tuberculum on lateroventral surface raises from the surface without an associated groove (character #106). An anteroposterior short ischiatic contribution to acetabulum (character #105) is shared by *Lusotitan* and Brachiosauridae. Other four features are recovered as synapomorphies of Brachiosauridae (characters #4, #8, #14 and #39), but it is not possible to test their presence in the available material of *Lusotitan*. Although the absence of information in some diagnostic elements for brachiosaurids (e.g. skull, ilium or the metapodials elements), it could be concluded, with some reservations, that *Lusotitan* is a member of Titanosauriformes, more related with the brachiosaurids than the Somphospondyli group.

11.7. DISCUSSION

11.7.1. *Lusotitan* within Neosauropoda

It is possible to recognize that *Lusotitan* shares several features with neosauropods, some of them considered as synapomorphy of this group (Wilson and Sereno, 1998; Upchurch et al., 2004). *Lusotitan* bears in the dorsal vertebra deep pleurocoels, common in neosauropods such as diplodocoids (excluding Dicraeosauridae, *sensu* Salgado et al., 1997) and basal macronarians (Wedel, 2003; Upchurch et al., 2004), and considered as synapomorphy for *Omeisaurus* + Neosauropoda by Wilson and Sereno (1998). The presence of deep excavations on the lateral face of the sacral centrum is other feature with a wide distribution within neosauropods, (e.g. Marsh, 1879; Hatcher, 1903; Osborn, 1904; Osborn and Mook, 1921; Janensch, 1950; Salgado, 1993; Curry Rogers and Forster, 2001; Suteethorn et al., 2009; Mocho et al., 2014), reversed in some derived titanosaurs (Upchurch, 1998). An important neosauropod feature is the presence of a subcircular proximal section of the tibia (Wilson and Sereno, 1998; Upchurch et al., 2004). Nevertheless, several putative stem-group of Neosauropoda such as *Lapparentosaurus* (Bonaparte, 1986), *Jobaria* (Wilson, 2002) or *Ferganosaurus* (Alifanov and Averianov, 2003) also bear this condition, and an accurate phylogenetic study is necessary in order to confirm the presence of a tibial circular proximal section as synapomorphy of Neosauropoda or of a more inclusive group. The plesiomorphic condition, a transversely compressed proximal end, is observed in non-neosauropods such as *Turiasaurus* (Royo-Torres et al., 2006; Royo-Torres and Upchurch, 2012), *Spinophorosaurus* (Remes et al., 2006), *Mamenchisaurus* (Ouyang and Ye, 2002), *Cetiosaurus oxoniensis* (Upchurch and Martin, 2003) or *Chuanjiesaurus* (Sekiya, 2011), but also present, in a convergent way, in some macronarians such as *Europasaurus* (Sander et al., 2006), and in more derived titanosauriforms such as *Malawisaurus* (Gomani, 2005), *Euhelopus* (Wiman, 1929, not significantly compressed), *Sauroposeidon* (Rose, 2007) or *Rapetosaurus* (Curry-Rogers, 2009). The astragalus of *Lusotitan* also shares some evolutionary novelties of neosauropods (e.g. Wilson and Sereno, 1998): the ascending process surpassing the anterior 2/3 of the astragalus, almost reaching the astragalus posterior margin and a wedge-shaped outline in anterior view. The plesiomorphic condition (ascending process limited to anterior two-thirds of astragalus) is common in non-neosauropod eusauropods such as *Turiasaurus* (Royo-Torres et al., 2006) or *Mamenchisaurus* (Young and Zhao, 1972).

11.7.2. *Lusotitan* within Macronaria

Incompleteness of *Lusotitan*, in particular of the dorsal vertebra, does not allow us to test with precision its assignation to Macronaria clade. Indeed, *Lusotitan* bears some features that could suggest its exclusion from Macronaria clade. Although the difficulty to test accurately the

morphology of the anterior articulation for the posterior dorsal centra (due to its weak state of preservation), *Lusotitan* seems to bears a slight convexity dorsally that transits to a slight concavity ventrally in the available middle or posterior dorsal vertebra. The opisthocoelous condition in every dorsal vertebrae is wide accepted as a synapomorphy of macronarians (or camarasauromorphs if *Haplocanthosaurus* is considered as a basal macronarian) (Salgado et al., 1997; Wilson, 2002; Upchurch et al., 2004; Carballido et al., 2011; D'Emic, 2012) and well-developed in basal macronarians such as *Camarasaurus* (e.g. Osborn and Mook, 1921) or *Lourinhasaurus* (Mocho et al., 2014). Nevertheless, strong convex anterior articulations that are common in macronarians (Wilson 2002; Upchurch et al., 2004), are not so pronounced in some titanosauriforms such as *Giraffatitan* (Janensch, 1950), *Muyelensaurus* (Calvo et al., 2007a), the putative Upper Jurassic titanosauriform of Damparis (assigned to "*Bothriospondylus*" by Lapparent, 1943) and it is almost absent in *Brachiosaurus altithorax* (FMNH P25107, Riggs, 1903). In particularly, *B. altithorax* seems to shares the same condition of *Lusotitan*: dorsal convexity in the anterior articulation that deflects posteriorly in ventral direction producing a concavity.

Other important condition in *Lusotitan* is the presence of dorsal bridged anterior chevrons, that is the plesiomorphic state relatively to the dorsal opened chevrons and is uncommonly shared by macronarians (Salgado et al., 1997; Wilson and Sereno, 1998; Upchurch et al., 2004) such as *Europasaurus* (Sander et al., 2006; Carballido and Sander, 2014), *Camarasaurus* (Osborn and Mook, 1921; Ostrom and McIntosh, 1966) and *Giraffatitan* (Janensch, 1950). The presence of this plesiomorphic state in *Lusotitan* were also identified in other macronarians such as some juvenile and subadult specimens of *Camarasaurus* (Maltese, 2002; McIntosh, 1996) and some Cretaceous Chinese titanosauriforms such as *Dongbeititan* (Wang et al., 2007), *Daxiatitan* (Lü et al., 2008) and *Xianshanosaurus* (Lü et al., 2009).

The *Lusotitan* pubis has an unusual morphology for a sauropod. Its general morphology is shared with that of some titanosauriforms such as *Futalognkosaurus* (Calvo et al., 2007b) or *Quiaowanlong* (You and Li, 2005). A short ischiatic articulation in the pubis (less than 1/3 of total pubis lenght) excludes *Lusotitan* from the long ischiatic articulation shared by macronarians (a synapomorphy of Macronaria *sensu* Wilson and Sereno, 1998, or a synapomorphy of Camarasauromorpha *sensu* Upchurch et al., 2004) and is also present in other titanosauriforms such as *Dongbeititan* (Wang et al., 2007) and *Quiaowanlong* (You and Li, 2005). However, several basal macronarians shows an intermediate state such as *Camarasaurus* (e.g. Osborn and Mook, 1921), *Tehuelchesaurus* (Carballido et al., 2011) and probably *Lourinhasaurus* (Mocho et al., 2014). Nevertheless, *Lusotitan*, *Futalognkosaurus* (Calvo et al., 2007b) and *Quiaowanlong* (You and Li, 2009) are far from an intermediate condition, showing short ischiatic articulations.

11.7.3. *Lusotitan* within Titanosauriformes

Although the difficulties to assign *Lusotitan* within Macronaria, it is possible to identify several features shared with the Titanosauriformes group. Nevertheless, it is important to take into account that recent phylogenetic hypotheses (D'Emic, 2012; Mannion et al., 2013; Carballido and Sander, 2014) are considering an early acquisition in sauropod evolution or a high degree of homoplasy in several traditional Titanosauriformes synapomorphies such as the lateral bulge of femur and the camellate tissue bone on presacral vertebrae.

One of the most characteristic features of Titanosauriformes is the presence of camellate bone tissue in presacral vertebrae, fact that it is not possible to test accurately on the *Lusotitan* type specimen. The only preserved presacral centrum shows an internal ramification in small cameras near the anterior articulation, at the base of the neural arch, suggesting the presence of this type of tissue as in *Giraffatitan* (Janensch, 1950). Nevertheless, an internal ramification near

the anterior and posterior articulation also occurs in *Lourinhasaurus* (Mocho et al., 2014) and *Camarasaurus* (Wedel, 2003).

The general caudal vertebrae morphology of *Lusotitan* is shared by Titanosauriformes. A marked dorsoventral compression in *Lusotitan* proximal-to-middle central (excluding MG 4985-2 and 3) is common in titanosauriforms, being present in *Giraffatitan* (Janensch, 1950), *Tastavinsaurus* (Canudo et al., 2008), *Brontomerus* (Taylor et al., 2011), *Borealosaurus* (You et al., 2004), *Malawisaurus* (Gomani, 2007), *Sauroposeidon* (Rose, 2007; D'Emic and Foreman, 2012), *Cedarosaurus* (Tidwell et al., 1999), *Xianshanosaurus* (Lü et al., 2009) and also in several titanosaurs (Upchurch et al., 2004). *Galveosaurus*, with an uncertain phylogeny (see Royo-Torres et al., 2006, 2009; Barco, 2009, 2010; Carballido et al., 2011; D'Emic, 2012; Royo-Torres and Upchurch, 2012, Carballido and Sander, 2014) also presents compressed centra. The dorsovental uncompressed centra of *Haplocanthosaurus* (Hatcher, 1903), *Camarasaurus* (Osborn and Mook, 1921), *Lourinhasaurus* (Mocho et al., 2014) and *Aragosaurus* (Sanz et al., 1987, Royo-Torres et al., 2014) distinguish them from *Lusotitan*. The most anterior caudal centra of *Lusotitan* have a slight concave posterior face as in the anterior caudals of the titanosauriform *Fusuisaurus* (Mo et al., 2006). However, the other preserved anterior caudal vertebrae of *Lusotitan* bear flat posterior articulations, common condition in basal macronarians and basal titanosauriforms such as *Camarasaurus* (e.g. Osborn and Mook, 1921), *Lourinhasaurus* (Mocho et al., 2014), *Tastavinsaurus* (Canudo et al., 2008), *Cedarosaurus* (Tidwell et al., 1999), *Aragosaurus* (Sanz et al., 1987; Royo-Torres et al., 2014); *Sauroposeidon* (D'Emic and Foreman, 2012), *Giraffatitan* (Janensch, 1950) and *Malarguesaurus* (González Riga et al., 2009). Some putative somphospondyls (*sensu* D'Emic, 2012) such as *Astrophocaudia* (D'Emic, 2013) and *Xianshanosaurus* (Lü et al., 2009) show a slight procoelic condition, but not so marked than in titanosaurs (Salgado et al., 1997; Upchurch et al., 2004; Mannion and Calvo, 2011). Caudals of *Lusotitan* could be easily distinguished from procoelic proximal caudals of titanosaurs, flagellicaudatians and some eusauropods forms (*Losillasaurus* and mamenchisaurids) (Salgado et al., 1997; Upchurch, 1998; Casanovas et al., 2001; Mannion and Calvo, 2011; Whitlock, 2011).

Other shared titanosauriform feature is the anterior displacement of the neural arches in the middle caudals (e.g. Salgado et al., 1997; You et al., 2006; D'Emic, 2012) present in *Lusotitan* and in the brachiosaurids *Giraffatitan* (Janensch, 1950), *Cedarosaurus* (Tidwell et al., 1999), *Venenosaurus* (Tidwell et al., 2001), and in the basal macronarian *Europasaurus* (Carballido and Sander, 2014). The non-neosauropod *Cetiosaurus oxoniensis* also presents an anterior displacement of the neural arch (Upchurch and Martin, 2003), but not so pronounced as in titanosauriforms.

The posterior projection of the caudal ribs surpassing the posterior face of the centrum in the anterior caudal vertebrae (except the firsts ones) is common in some titanosauriforms such as *Giraffatitan* (Janensch, 1950), *Cedarosaurus* (Tidwell et al., 1999), *Astrophocaudia* (D'Emic, 2013); *Tastavinsaurus* (Canudo et al., 2008; Royo-Torres, 2009), *Sonorasaurus* (Ratkevitch, 1999), *Andesaurus* (Mannion and Calvo, 2011), *Malawisaurus* (Gomani, 2005), *Trigonosaurus* (Campos et al., 2005), *Fusuisaurus* (Mo et al., 2006), *Sauroposeidon* (D'Emic and Foreman, 2012) and *Phuwiangosaurus* (Suteethorn et al., 2009) and could be a synapomorphy for titanosauriforms (as noted Mannion and Calvo, 2011). Posterior orientated caudal ribs are also present in *Galveosaurus*, considered by some authors as a basal eusauropod (Sánchez-Hernández, 2005; Royo-Torres et al., 2006; a putative basal macronarian *sensu* Carballido et al., 2011 and Carballido and Sander, 2014), *Losillasaurus* (Casanovas et al., 2001) and *Cetiosaurus oxoniensis* (pers. observ., PM). Mannion et al. (2013) proposed a new character related with the posterior orientation of the caudal ribs, considering that some taxa bear particular long caudal ribs, surpassing the posterior articulation (excluding the posterior ball). This condition is present in *Lusotitan* such as in the brachiosaurids

Abydosaurus, *Giraffatitan* and *Cedarosaurus* (Mannion et al., 2013), or other more derived forms such as *Tastavinsaurus* (Canudo et al., 2008; Royo-Torres, 2009) or *Andesaurus* (Mannion and Calvo, 2011). Basal macronarians bear mainly lateral directed caudal ribs, such *Lourinhasaurus* (Mocho et al., 2014), *Camarasaurus* (e.g. Osborn and Mook, 1921), *Europasaurus* (Carballido and Sander, 2014) and *Aragosaurus* (Sanz et al., 1987; Royo-Torres et al., 2014).

Anterior dorsal ribs with this morphology were considered a synapomorphy of Titanosauriformes (Wilson, 2002), or of *Tehuelchesaurus* + Titanosauriformes (D'Emic, 2012). Lapparent and Zbyszewski (1957) referred rib fragments with plate morphology for *Lusotitan atalaiensis*, but only one of the currently available fragments presents this type of morphology. Nevertheless, this fragment could not be assigned to an anterior dorsal rib.

The haemal channel is deeper than one half of the total length of the chevron in *Lusotitan*. This condition is considered a synapomorphy of Titanosauria (Wilson, 2002) but also present in several titanosauriforms such as *Europasaurus* (Sander et al., 2006; Carballido and Sander, 2014), *Tastavinsaurus* (Canudo et al., 2008; Royo-Torres, 2009), *Giraffatitan* (Janensch, 1950), *Cedarosaurus* (Tidwell et al., 1999) and probably *Huanghetitan* (You et al., 2006). The phylogenetic hypothesis proposed by D'Emic (2012) considered this feature as a synapomorphy of Titanosauriformes.

In spite of the incompleteness of the anteromedial process of the ulna of *Lusotitan*, is possible to verified that this process is more developed than the lateral one, a feature common in titanosauriforms (D'Emic, 2012) and in some basal macronarians such as *Lourinhasaurus* (Mocho et al., 2014). An abrupt transition between the lateral and dorsal margin of the humerus producing a subsquared outline is considered a synapomorphy for Somphospondyli by several authors (Wilson, 2002) or for a more inclusive macronarian group (*sensu* Carballido et al., 2011; D'Emic, 2012). Nevertheless, we considered that the most part of non-Somphospondyli members have a rounded dorsolateral corner (also noted by Mannion and Calvo, 2011) such as *Giraffatitan* (Janensch, 1961), *Brachiosaurus* (Riggs, 1903), *Cedarosaurus* (Tidwell et al., 1999), *Camarasaurus* (e.g. Mook and Osborn, 1921; Ostrom and McIntosh, 1966), *Tehuelchesaurus* (Carballido et al., 2011) and *Lourinhasaurus* (Mocho et al., 2014). *Lusotitan* shares with Titanosauriformes the absence of a marked tibial scar on the fibula, considered a synapomorphy of them (D'Emic, 2012). Some characters generally present in Somphospondyli such as a well-developed proximal medial corner, the presence of ventrolateral ridges on anterior and middle caudal centra, a pronounced olecranon process, undivided posterior fossa of astragalus and a transversely short astragalus (Wilson, 2002; Carballido et al., 2011) are absent in *Lusotitan*.

11.7.4. *Lusotitan* status

Lusotitan atalaiensis bears several exclusive features and an exclusive combination of characters. Antunes and Mateus (2003) proposed a diagnosis for this taxon, discussed and revised by Mannion et al. (2013). From the six proposed autapomorphies proposed by Mannion et al. (2013), four of them are considered herein for the proposed revised diagnosis of *Lusotitan atalaiensis*: *i*) caudal ribs with dorsal convex margins, *ii*) anterior-to-middle caudal postzygapophyses with transversely compressed form, elongate processes that project well beyond the posterior margin of the neural arch; and *iii*) no vertical groove extending up the shaft between the lateral and medial malleoli of the tibia.

Mannion et al. (2013) also considered as autapomorphic the presence of an elongated transverse pit in posterior and anterior articulations of caudal vertebrae. As it was described, the morphology of this pits changes along the tail, appearing in MG 4985-7. Pits in the articulations of caudal vertebrae also appears in several other sauropods such as *Lapparentosaurus*, *Spinophorosaurus* or *Cetiosaurus oxionensis* (pers. observ., PM) which could be transverse

elongated. Here, it is proposed the presence of a transverse elongated or T-shaped pits in the middle-posterior caudal vertebrae as a reformulation of this autapomorphy of *Lusotitan*.

Mannion et al. (2013) referred as diagnostic of *Lusotitan atalaiensis* the presence of a shoulder-like region lateral to the base of the spine between pre- and postzygapophyses at anterior-middle caudals. This structure corresponds to a lamina herein interpreted as the lat. sprl that comes from the prezygapophyses deflecting to the lateral face of the neural spine and borders ventrally a smooth fossa on the base of the neural spine lateral face. This type of structure is also observed in other sauropods such as *Europasaurus* (Carballido and Sander, 2014, fig. 27), or in the Praia de Areia Branca specimen (Yagüe et al., 2006). In *Europasaurus*, this structure is not so pronounced as in *Lusotitan* and the Praia de Areia Branca sauropod. The Praia de Areia Branca sauropod, that is still undetermined, shares this condition, but does not correspond to *Lusotitan* because the absence of a dorsoventral compressed anterior and middle caudal vertebrae and the presence of anterior and middle bridged chevrons.

The two recovered sacral neural spines bear several particular features. The morphology of spdl seems to be exclusive of *Lusotitan* with an interruption at spine midheight. Unfortunately, spdl is fractured at the base, and it is difficult to obtain the reliable morphology for this lamina. New material assignable to *Lusotitan* is needed to robustly consider this condition as diagnostic of this taxon. Other recognizable feature in the most anterior sacral spine is the presence of a pronounced and lateral projection of ventral section of the spol observed in posterior view (Fig. 11.4d) considered here as autapomorphy of *Lusotitan atalaiensis*.

The pubis is one of the most interesting elements of *Lusotitan*, presenting uncommon features within sauropods, and particularly, within Brachiosauridae. The orientation and the morphology of the pubis are considered here exclusive of *Lusotitan*. Three autapomorphies could be formulated: an anterior orientation of the pubis blade, a circular anterodistal termination of pubis blade and short ischiatic peduncle, although the last one is shared by some Chinese Early Cretaceous somphospondylians such as *Qiaowanlong* (You and Li, 2009). In the pubis, it was also identified a circular process in the acetabulum surface, but it is not clear what may be their origin and more material is needed to assess its systematic significance.

The tibia of *Lusotitan* bears two autapomorphies considered by Mannion et al. (2013). The ventral orientation of the cnemial crest apex it also proposed as autapomorphic of this taxon. This orientation of the cnemial crest is uncommon in sauropods and is absent in several macronarians of the Upper Jurassic and Lower Cretaceous: *Giraffatitan* (1961), *Tastavinsaurus* (Canudo et al., 2008; Royo-Torres, 2009; Royo-Torres et al., 2012), *Euhelopus* (Wilson and Upchurch, 2009), *Lourinhasaurus* (Mocho et al., 2014) and *Camarasaurus* (e.g. Ostrom and McIntosh, 1966). Other features proposed here as autapomorphies of *Lusotitan* are an acute lateral margin of the shaft of the tibia, bordered by dorsoventral smooth grooves; and an abrupt transition between the dorsal surface of the articular surface of the ascending process and the lateral surface of the tibial shaft that are unknown in other sauropods.

The phylogenetic hypothesis recovered in this study also helps to identify a few local autapomorphies for *Lusotitan*, such as the presence of bridged proximal chevrons and a short ischiatic peduncle (within Macronaria they are only shared, convergently, by some Chinese Cretaceous titanosauriforms).

11.7.5. *Lusotitan*, brachiosaurid affinities and comparisons

Brachiosauridae have been recovered in some recent cladistic based phylogenies as a monophyletic clade (e.g. D'Emic, 2012; Carballido and Sander, 2014; Mannion et al., 2013). This assignation is supported by the phylogenetic hypothesis proposed here based in Upchurch et al. (2004) and D'Emic (2012). Several synapomorphies have been proposed for this clade, but

a couple of them could not be test in the available material of *Lusotitan*. One of those features corresponds to the presence of an anteroposteriorly short pubic proximal plate only observed in *Giraffatitan*, *Europasaurus* and *Venenosaurus* and unknown for other putative brachiosaurids such as *Cedarosaurus*, *Brachiosaurus* and *Abydosaurus* (D'Emic 2012). The Upper Jurassic sauropod of Damparis (Lapparent, 1943) also bears an anteroposterior short pubic proximal plate as well as the basal titanosauriform *Tastavinsaurus* (Royo-Torres, 2009). The most recent phylogenetic analyses proposed distinct phylogenetic positions for *Tastavinsaurus*: a basal macronarian (Carballido et al., 2011; Carballido and Sander, 2014); a brachiosaurid (Royo-Torres et al., 2012, 2014; Mocho et al., 2014), or a more derived form than brachiosaurids (Canudo et al., 2008; Royo-Torres et al., 2012, 2014; D'Emic, 2012; Mannion et al., 2013; Mocho et al., 2014). In some analyses, *Tastavinsaurus* is included in monophyletic clade with other Lower Cretaceous titanosauriforms such as *Cedarosaurus* and *Venenosaurus*, named Laurasiformes (Royo-Torres et al., 2012).

Mannion et al. (2013) obtained as a synapomorphy of Brachiosauridae the presence of pneumatic fossae or foramina in the lateral face of anterior caudal vertebrae. For D'Emic (2012), the presence of these fossae or foramina is a synapomorphy of a more inclusive group within Brachiosauridae, that is composed by *Giraffatitan* + ((*Brachiosaurus* + (*Abydosaurus*, *Cedarosaurus*, *Venenosaurus*)). Although these authors considered that this condition is absent in anterior caudal vertebrae of *Lusotitan*, a depression is described below the transverse process of CdA (MG 4985-2) perforated by a shallow foramina (long axis ≈10mm) and also present in CdB (MG 4985-3) and CdC (MG 4985-4). This feature has been recognized in several putative brachiosaurids such as *Abydosaurus*, *Giraffatitan*, *Venenosaurus* or *Cedarosaurus* (e.g. Tidwell et al., 1999; D'Emic 2012; Mannion et al., 2013), and absent in *Brachiosaurus* and *Sonorasaurus* (*sensu* Mannion et al., 2013), showing an inconsistent distribution within Brachiosauridae. Other sauropods also presents this condition such as *Apatosaurus*, *Malawisaurus*, *Alamosaurus* and *Diplodocus* (Mannion et al., 2013), *Xianshanosaurus* (Lü et al., 2009), *Tastavinsaurus* (Royo-Torres, 2009; Royo-Torres et al., 2014) and *Andesaurus* (Mannion and Calvo, 2011). The condition in *Diplodocus* (Osborn, 1899; Hatcher, 1901), *Tornieria* (Remes, 2006) or *Barosaurus* (Lull, 1919; McIntosh, 2005) is particularly distinct, because wide and deep pleurocoels, with marked borders, develops in the lateral face of anterior caudal vertebrae of these taxa.

Excluding *Europasaurus*, which is considered a basal macronarian by Carballido et al. (2011) and Carballido and Sander (2014), brachiosaurids are featured by relative longer forelimb as well as the eusauropod *Atlasaurus* (Mombaron, 1999). In the case of *Lusotitan*, it is not possible to know the humerus length/femur length ratio. Nevertheless, the presence of a complete left radius and tibia allows testing indirectly this feature in *Lusotitan*. The radius is longer than tibia (ratio radius:tibia length is ≈1,05) in *Lusotitan*. In sauropods, this ratio is generally less than 1 (i.e. tibia higher than radius) such as *Camarasaurus* (e.g. Gilmore, 1925; Ikejiri, 2004), *Mamenchisaurus* (Ouyang and Ye, 2002); *Ferganasaurus* (Alifanov and Averianov, 2003), *Bellusaurus* (Dong, 1990) or *Rapetosaurus* (Curry Rogers, 2009). Within Brachiosauridae, only *Cedarosaurus* preserves radius and tibia. *Cedarosaurus* has a tibia taller than radius but this value (0,91) is particularly high for a sauropod. High values are also identified in the camarasauromorph *Lourinhasaurus* (≈0,92) and the putative somphospodylian *Tastavinsaurus* (1, Royo-Torres, 2009) and basal eusauropod *Atlasaurus* (1,1, Mombaron, 1999).

The humerus is particular similar with brachiosaurids humeri such as those of *Brachiosaurus* (Riggs, 1903); *Giraffatitan* (Janensch, 1961) or the putative brachiosaurid of Damparis (Lapparent, 1943), with a dorsoventrally restricted and pronounced deltopectoral crest. A pronounced deltopectoral crest is also present in turiasaurs, but the brachiosaurids do not bears the pronounced medial deflection of the proximal end that features the members of Turiasauria (Royo-Torres et al., 2006). D'Emic (2012) referred as synamopomorphic of *Brachiosaurus* + (*Abydosaurus*, *Cedarosaurus*, *Venenosaurus*) group, the presence of a rounded dorsolateral

corner in the humerus. This condition is also shared by *Lusotitan*. Nevertheless, it is considered here that a rounded dorsolateral corner in the humerus is the plesiomorphic condition in non-somphospondylian titanosauriforms, as suggested Wilson (2002), and present in *Giraffatitan* (Janensch, 1961), *Lourinhasaurus* (Mocho et al., 2014), *Tehuelchesaurus* (Carballido et al., 2011), and *Camarasaurus* (Ostrom and McIntosh, 1966; Osborn and Mook, 1921; Ikejiri, 2004).

Lusotitan could be easily distinguished from other putative brachiosaurids. It differs from *Giraffatitan* and *Cedarosaurus* by the presence of a ratio of centrum length to centrum height for the proximal caudals > 0,6 or bridged chevrons (absent in all known brachiosaurids). In the ischium of *Giraffatitan* and *Venenosaurus* the long axis of the ischiatic blade passing dorsally to the acetabulum (Janensch, 1961; Tidwell et al., 2001) differs from the condition of *Lusotitan* and the sauropod of Damparis. *Brachiosaurus* presents several similarities with *Lusotitan*, sharing the morphology of the anterior facet of the posterior dorsal centra and the general morphology of humerus. Unfortunately, it is difficult to the test the grade of similarity between both taxa, because the absence of well-preserved dorsal vertebrae in *Lusotitan* specimen, and the absence of several elements in *Brachiosaurus*, which are diagnostic in *Lusotitan* such as the tibia and the pubis. *Brachiosaurus* presents a pronounce prdl on its anterior vertebrae (Riggs, 1903; Mannion et al., 2013) that is not shared by *Lusotitan*.

Europasaurus was considered a brachiosaurid (*sensu* D'Emic, 2012; Mannion et al., 2013), but new published data suggested that *Europasaurus* correspond to a basal macronarian (Carballido et al., 2011; Carballido and Sander, 2014). This taxon could be distinguished of *Lusotitan* by the absence of any depressions or foramina in the lateral or ventral face of anterior-middle caudal vertebrae, anterior caudal ribs are mainly lateral directed and do not extends beyond the posterior articulation and the absence of crest-like anterior trochanter. Other important difference between *Lusotitan* and *Europasaurus* is the presence of a dorsoventral compression in dorsal and anterior-middle caudal centra in the former one.

Lusotitan also shows important morphological affinities with the Damparis sauropod related by Lapparent (1943) to "*Bothriospondylus madagascariensi*s". Large pleurocoels on dorsal vertebrae, straight proximal margin of fibula, trapezoidal astragalus and slight opistocoelic condition in most posterior dorsal central are some shared features in both taxa. Damparis sauropod also shares several common features in Titanosauriformes or Brachiosauridae such as the general teeth morphology, the humeral gracility and lateral bulge of the femur (some of them already noted by Mannion, 2010). Nevertheless, the systematic revision of this material is needed.

Beyond the Upper Jurassic sauropods, *Lusotitan* could be distinguished of Lower Cretaceous brachiosaurids of North America, which they may be forming a monophyletic clade (D'Emic, 2012). *Cedarosaurus* bears some features not observed in *Lusotitan* such as a ridge on the lateral surface of the middle caudals located at the junction of the neural arch (Royo-Torres et al., 2012), dorsal pleurocoels setting in a fossa (Royo-Torres et al., 2012; Mannion et al., 2013), and medially extending deltopectoral crest (Tidwell et al., 1999: fig. 7).

11.7.6. The Iberian Upper Jurassic titanosauriform record

In spite of the difficulties shown by the available material of *Lusotitan* lacking several diagnostic elements in order to proceed an accurate phylogenetic approach, if the proposed phylogenetical hypothesis is correct, *Lusotitan* is a basal titanosauriform. *Lusotitan* is also the only member of Titanosauriformes defined for the Iberian Upper Jurassic. Other putative Iberian Upper Jurassic titanosauriforms are *Galveosaurus* (Sanchéz-Hernadez, 2005) and *Aragosaurus* (Sanz et al., 1987; Royo-Torres et al., 2009, 2012, 2014; Canudo et al., 2001, 2012; D'Emic, 2012). *Aragosaurus* was firstly related with the camarasaurids (Sanz et al., 1987) but some authors related it to basal Titanosauriformes (Canudo et al., 2001, 2012; D'Emic, 2012). *Aragosaurus* bears some

features previously considered as synapomorphies of Titanosauriformes, such as the lateral bulge on the femur or posteriorly unexpanded distal section of the ulna (shared with *Lourinhasaurus*). Nevertheless, recent phylogenetic approaches suggest that *Aragosaurus* corresponds to a basal macronarian (Mannion et al., 2013; Royo-Torres et al., 2014). The pelvic griddle and the caudal vertebrae of *Aragosaurus* show important similarities with *Camarasaurus* and *Lourinhasaurus*, both Upper Jurassic basal non-titanosauriforms macronarians (Upchurch et al., 2004; Mocho et al., 2014; Royo-Torres et al., 2014). D'Emic (2012) noted for the presence of a titanosaurian synapomorphy: the absence of emargination distal of the pubic peduncle, but this sector of ischium is not complete (Royo-Torres et al., 2014, pers. observ.,PM). *Aragosaurus* is marked distinct from *Lusotitan* based on the orientation of the pubis, gracility of the humerus, and the position of neural arches in the middle caudals. Furthermore, the ischia in *Aragosaurus* bears a lateral groove associated to a muscle scar (pers. observ., PM), present in non-titanosauriforms, and not shared by *Lusotitan*.

Galveosaurus (Sanchéz-Hernandez, 2005; Barco, 2009) is other taxon considered unstable in available phylogenetic proposals. *Galveosaurus* was considered as a member of "Cetiosauridae" (Sanchéz-Hernandez, 2005); a Turiasauria (Royo-Torres et al., 2006, 2009, 2012; Royo-Torres and Upchurch, 2012); a basal macronarian (Barco 2009, 2010; Carballido et al., 2011) or a putative titanosauriform (D'Emic, 2012). More material is needed to provide a more precise phylogenetic approach for *Galveosaurus*. *Galveosaurus* shares with *Lusotitan* and other basal titanosauriforms, the presence of dorsoventral compressed caudal vertebrae, anterior displacement of the neural arches in middle caudals, the absent of a lateral groove in the ischium, and dorsoventrally restricted deltopectoral crest. In this moment, we consider particularly difficult to distinguished *Galveosaurus* from *Lusotitan*, and we do not exclude the possibility of *Galveosaurus herreroi* be a junior synonymous of *Lusotitan atalaiensis*. Nevertheless, a detailed phylogenetic analysis for *Galveosaurus* and the discovery of new material will help to test the hypothesis of the synonymy between both taxa.

The Portuguese Upper Jurassic are rich in titanosauriform-like fossil remains: *i*) Guimarota mine titanosauriform teeth from Kimmeridgian (Rauhut, 2000); *ii*) the tooth from Ourém (Sauvage 1897-98; Lapparent and Zbyszewski, 1957); *iii*) a titanosauriform tooth with unknown locality assigned to *Apatosaurus* sp. by Lapparent and Zbyszewski (1957, pl.12, fig.1); *iv*) the Areia Branca femur, with important lateral bulge and with a marked anteroposteriorly compressed diaphysis (Lapparent and Zbyszewski, 1957), and *v*) unpublished material from the Tithonian of the Lusitanian basin (work in progress).

From the Tithonian-early Beriasian of the Villar del Arzobispo Formation in Spain it was also found some teeth that could be assigned to Titanosauriformes (Sanz, et al., 1999; Sanchéz-Hernandez, 2007; Royo-Torres et al., 2014).

11.7.7. Upper Jurassic Titanosauriformes Paleobiogeography

Titanosauriformes was defined by Salgado et al. (1997) and since then several new occurrences from Upper Jurassic and Early Cretaceous was included within this group. Several topics concerning the group were considered by several authors (e.g. Carballido et al., 2011; D'Emic, 2012; Royo-Torres et al., 2012; Mannion et al., 2013; Carballido and Sander, 2014) in order to understand the evolution of this group and their paleobiogeography. The early phase of Titanosauriformes diversification probably starts in late Middle Jurassic (e.g. Rauhut, 2006; D'Emic, 2012) but the first reliable fossil evidences are dated from the Upper Jurassic (e.g. Riggs, 1903; Janensch, 1936; Lapparent and Zbyszewski, 1957). The Upper Jurassic record suggested for titanosauriforms a wide paleogeographical distribution including Laurasia and Gondwana territories (Rauhut, 2006) as occurring in diplodocids (e.g. Whitlock, 2011) and basal non-titanosauriforms macronarians (Carballido et al., 2011, Mocho et al., 2014; Royo-Torres et al., 2014).

In the Upper Jurassic fossil record of Laurasia, titanosauriforms are represent by *Lusotitan* (Lapparent and Zbyszewski, 1957; Antunes and Mateus, 2003) and *Brachiosaurus* (Riggs, 1903). The sauropod of Damparis ("*Bothriospondylus madagascariensis*" *sensu* Lapparent, 1943; Mannion, 2010), if accepted as a titanosauriform (Mannion, 2010; Mannion et al., 2013) also increases the number of titanosauriform taxa of the Laurasia Upper Jurassic sauropods. Barrett et al. (2010) considered an incomplete humerus (NHMUK 44635) found in Kimmeridgian-lower Tithonian sediments of the Clay Formation (Dorset, United Kingdom) and previously referred as "*Pelorosaurus humerocristatus*" as a member of Brachiosauridae, establishing a new taxon, *Duriatitan humerocristatus*. It is particularly hard to obtain a strongly supported phylogenetic proposal for this taxon due to its incompleteness, and we prefer to consider *Duriatitan* as a Sauropoda *incertae sedis* up to the discovery of more material.

Ye et al. (2005) identified a putative brachiosaurid, *Daanosaurus*, in the Chinese Upper Jurassic, and related to "Bellusaurinae". Li et al. (2011) recover it in a close relationship with *Mamenchisaurus*. D'Emic (2012) considered *Daanosaurus* as a macronarian member by the presence of the opisthocoelic condition in the most posterior dorsal vertebra. This condition is also shared by some Middle-to-Upper Jurassic taxa with distinct phylogenetic positions (outside of Neosauropoda clade, Wilson, 2002; Upchurch et al., 2004; Remes, 2006) such as *Mamenchisaurus* and *Omeisaurus*; and the Middle Jurassic *Bellusaurus* (Dong, 1990) and *Abrosaurus* (Ouyang, 1989) firstly assigned to Macronaria. The placement of *Bellusaurus* within Macronaria was supported by Upchurch et al. (2004) or Sekiya (2011) but rejected by Royo-Torres et al. (2012), Royo-Torres and Upchurch (2012) and Li et al. (2011) which recovered as a eusauropod non-neosauropod. The phylogeny of *Daanosaurus* seems to be uncertain and needs to be revised as well as the stratigraphic position. Ye et al. (2005) attribute this taxon to the Upper Jurassic but other authors (Remes, 2007; Li et al., 2011) place this taxon in the Lower Shaximiao Fm. dated of Bathonian (Middle Jurassic), the same formation of *Bellusaurus* and *Abrosaurus*. If the relation of *Daanosaurus* to Titanosauriformes is not sustained in future phylogenetic analysis, the Upper Jurassic East Asian territory still lacks any recognized titanosauriform during the Upper Jurassic as well as any neosauropod form (e.g. Wilson and Upchurch, 2009). This fact supports the model for East Asian Isolation during the Middle Jurassic (Bathonian or early Callovian) to Early Cretaceous (e.g. Milner and Norman 1984; Russell and Zheng, 1993; Upchurch, 1995, 2002; Barrett et al., 2002; Rauhut, 2006; Wilson and Upchurch, 2009) resulting in the development of endemic eusauropod faunas (e.g. Wilson and Upchurch, 2009).

From the Gondwanan Upper Jurassic, some titanosauriforms have been referred such as *Giraffatitan* (Janensch, 1929) and, possibly, *Janenschia* (see McIntosh, 1990b; Wild, 1991; Wilson, 2002; Upchurch et al., 2004). Finally, Rauhut (2006) identified a new brachiosaurid in Cañadón Calcareo Formation in Chubut (Argentina) from Tithonian sediments. This author considered it as a titanosauriform by the presence of anterior displacement of the neural arches on middle caudals, and as a brachiosaurid by the slenderness of humerus and radius and the dorsoventral compressed dorsal centra. Mannion et al. (2013) considered it as an indeterminate macronarian. Some authors related *Tehuelchesaurus* to Titanosauriformes (Rauhut, 2002; Rauhut et al., 2005) but the most recent phylogenies recovered it as a camarasauromorph (Carballido et al., 2011; Mannion et al., 2013; Carballido and Sander, 2014; Mocho et al., 2014; Royo-Torres et al., 2014).

Titanosauriforms seem to acquire a wide paleobiogeographic distribution along the Upper Jurassic, being present in North America, Europe, Africa. The apparent absence of titanosauriforms (and neosaurods in general) in the Upper Jurassic of East Asian territory (e.g. Wilson and Upchurch, 2009) suggests that the origin and the dispersion of this group of sauropod might occur after the East Asian Isolation. Nevertheless, the phylogenetic revision of *Bellusaurus* might add new information about the presence of neosauropods in East Asia territory.

11.8. CONCLUSIONS

Lusotitan atalaiensis is one of the first sauropod taxon established for the Iberian Upper Jurassic and classically considered as brachiosaur. In a recent study (Mannion et al., 2013), *Lusotitan* was included for the first time in a cladistics analysis, concluding that this taxon is as a Macronaria and a brachiosaurid with doubt. Nevertheless, the reassessment of all material assigned to the *Lusotitan atalaiensis* lectotype allows completing the description of several elements (dorsal ribs, sacral vertebrae, chevrons, fibula, pubis and ischium) as well as the reinterpretation of some elements, resulting in new information for the morphological data matrices.

This analysis corroborates the validity of *Lusotitan atalaiensis*, providing a reviewed diagnosis supplementing previous ones (Antunes and Mateus, 2003; Mannion et al., 2013). *Lusotitan* is supported by the following autapomorphies: (1) spdl does not reach the distal process on sacral neural spines; (2) small lateral projection of spol at midheight of the most anterior sacral spine; (3) the caudal rib on the anteriormost caudal vertebra is convex dorsolaterally in posterior view; (4) anterior-to-middle caudal postzygapophyses transversely compressed, constituting elongate processes that project well beyond the posterior margin of the neural arch; (5) the presence of transverse elongated or T-shaped pits in the middle caudal vertebrae; (6) circular fossae in the ventral face of the middle caudals, anteriorly located to the chevron facets; (7) presence of proximal bridged chevrons; (8) short ischiatic peduncle; (9) pubis blade with a marked anterior orientation; (10) anterior margin of pubis peduncle bearing a rounded projection; (11) pubis peduncle of the ischium constricted in anterior view; (12) tibia strongly bowed laterally; (13) no vertical groove extending up the shaft between the lateral and medial malleoli of the tibia; (14) tibial crest ventrally directed; (15) acute lateral margin of the tibia, bordered by dorsoventral smooth grooves; (16) abrupt transition between the dorsal surface of the articular surface of ascending process and the lateral surface of the tibial shaft.

The proposed phylogenetic hypothesis incorporates the new information provided for *Lusotitan* in two comprehensive data matrices for sauropod phylogeny (Wilson, 2002; Upchurch et al., 2004) and the recent published data matrix of D'Emic (2012) focused in Titanosauriformes. All analyses recovered *Lusotitan* as a macronarian. *Lusotitan* bears unequivocal affinities with Titanosauriformes, and in particular, with the Brachiosauridae *Brachiosaurus*, *Giraffatitan*, *Venenosaurus*, *Cedarosaurus* and *Abydosaurus*, such as the general morphology of the caudal vertebrae (e.g. orientation of caudal ribs, dorsoventral compressed caudal centra), humerus (gracility, pronounced and short deltopectoral crest), and a putative high humerus/femur length ratio (inferred by the high radius/tibia length ratio).

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11.10. REFERENCES

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CHAPTER 12

A new Upper Jurassic macronarian sauropod (Dinosauria) from the Lusitanian Basin

A new Upper Jurassic macronarian sauropod (Dinosauria) from the Lusitanian Basin

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12.1. INTRODUCTION

The sauropod faunas of the Portuguese Upper Jurassic of the Lusitanian Basin have been subject of recent analysis (e.g. Mannion et al., 2012, 2013; Mateus et al., 2014; Mocho et al., 2014a), with an important improvement of the phylogeny of this group in the Iberian realm. The Portuguese fossil record of sauropods is known from the last part of the 19th century (Sauvage, 1897-98). Lapparent and Zbyszewski (1957) erected a new *Brachiosaurus* species, *Brachiosaurus atalaiensis*, for a specimen from Peralta (Lourinhã), and a new species of *Apatosaurus*, *Apatosaurus alenquerensis*, for several occurrences including a relative complete sauropod from Moinho do Carmo (Alenquer). In the last decades of the 20th century up today, several works emerge in order to revise classical specimens and to study new ones. Dantas et al. (1998) revised the original material of *A. alenquerensis* plus one new specimen from Porto Dinheiro (Lourinhã, Dantas et al., 1992) proposing a new genus, *Lourinhasaurus*. Later, the Porto Dinheiro specimen was considered as a different form from that of Moinho do Carmo, defined as a new diplodocid, *Dinheirosaurus lourinhanensis* Bonaparte and Mateus, 1999. Antunes and Mateus (2003) considered that the Peralta sauropod was not member of *Brachiosaurus* and proposed a new generic assignation, *Lusotitan atalaiensis*.

For more than one decade, the phylogenetic relationships of these three sauropod remained uncertain, but recent cladistic analyses (Mannion et al., 2012, 2013; Mocho et al., 2014a) have tried to put these taxa in a phylogenetic context. *Dinheirosaurus*, firstly related to the Diplodocidae clade (Bonaparte and Mateus, 1999), was considered as non-diplodocine diplodocid close related to *Supersaurus* (Mannion et al., 2012; Tschopp and Mateus, 2013) or a more derived diplodocid such as *Barosaurus*, *Tornieria* or *Diplodocus* (Rauhut et al., 2005; Whitlock, 2011). Several specimens with diplodocine affinities have been reported for the Portuguese Upper Jurassic (Mannion et al., 2012; Mocho et al., 2014b).

Lourinhasaurus alenquerensis was considered a potential new species of *Camarasaurus* (McIntosh, 1990a, b; McIntosh et al., 1996b; Wilson and Sereno, 1998); a basal eusauropod (Upchurch et al., 2004); a basal macronarian (Royo-Torres et al., 2006; Barco, 2010), or a non-macronarian neosauropod (Royo-Torres and Upchurch, 2012; Royo-Torres et al., 2012). The reassessment of *L. alenquerensis* lectotype, including the description of not previously described and figured elements, allow obtaining a new phylogenetic approach, suggested *Lourinhasaurus* as a member of Camarasauridae, which includes *Camarasaurus* and *Tehuelchesaurus* (Mocho et al., 2013a, 2014a). Finally, Mannion et al. (2013) redescribed some elements of type specimen of *Lusotitan atalaiensis*, proposing a new diagnosis and one of the first cladistic analyses for this taxon, recovering it as a basal Macronaria, member of Brachiosauridae with doubt.

Zby atlanticus was recently defined by Mateus et al. (2014) based on a specimen composed by an almost complete forelimb and some axial and scapular girdle elements found in Vale de Pombas (Lourinhã). This specimen (ML 368) was considered as *Camarasaurus* sp. (Mateus, 2005), and as *Turiasaurus riodevensis* (Mateus, 2009), being related with the Turiasauria clade (Mateus, 2009; Mateus et al., 2011; Royo-Torres and Upchurch, 2012; Mocho et al., 2012; Mateus et al., 2014). Several new specimens have been reported and described for the Lusitanian Basin Upper Jurassic, being related to Turiasauria (Royo-Torres et al., 2006, 2009; Mateus, 2009; Ortega et al., 2010; Mocho et al., 2012), Diplodocidae (Mannion et al., 2012; Mocho et al., 2014b) and Macronaria (Yagüe et al., 2006; Mocho et al., 2013b, c). Besides the apparent presence of exclusive sauropod forms in the Upper Jurassic of the Lusitanian Basin, the identified taxa belong to groups represented by closely related forms at the Morrison (USA) and Villar del Arzobispo (Spain) Formations. Some authors suggested that this faunal composition results from an incipient process of vicariance (Ortega et al., 2013; Hendrickx and Mateus, 2014).

Herein, a new basal macronarian (SHN 181) from Praia da Amoreira-Porto Novo Formation is reported and described in detail. This new sauropod increases the known paleobiodiversity of Macronaria for the Iberian Upper Jurassic, composed by *Lourinhasaurus*, *Lusotitan*, *Aragosaurus* and possibly *Galveosaurus* (Antunes and Mateus, 2003; Carballido et al., 2011; Mannion et al., 2013; Carballido and Sander, 2014; Mocho et al., 2013a, b, c, 2014; Royo-Torres et al., 2014).

12.2. ANATOMICAL ABBREVIATIONS

aa, accessory articulation; aca, anterior chevron articulation; acet, acetabulum; acr, acromial ridge; asp, ascending process; aspa, anterior surface for the ascending process; at, anterior trochanter; au, autapomorphy; av, anterior view; bu, bulde; caa, calcaneum articular surface; cc, cnemial crest; cof, coracoid foramen; cr, caudal rib; dv, dorsal, view; ep, epicondyle; f, foramina; fia, fibular articular surface; fic, fibular condyle; ft, fourth trochanter; gl, glenoid; gr, groove; ilped, iliac peduncle; lv, left view; lt, lateral trochanter; paf, posterior astragalar fossa; pafc, posterior astragalar fossa crest; pca, posterior chevron articulation; poap, postacetabular process; posl, postspinal lamina; prdl, prezygadiapophyseal lamina; prsl, prespinal lamina; prz, prezygapophysis; pv, posterior view; pvp, posteroventral process; rv, right view; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprf, spinoprezygapophyseal fossa; sprl, spinoprezygapophyseal lamina; srf, sacral rib facet; sym, symphysis; tia, tibial articular surface; tic, tibial condyle; tprl, intraprezygapophyseal lamina; tb, tuberosity; vv, ventral view.

12.3. INSTITUTIONAL ABBREVIATIONS

MG, Museu Geológico do Laboratório Nacional de Energia e Geologia, Lisboa, Portugal; ML, Museu da Lourinhã, Lourinhã, Portugal; SHN, Sociedade de História Natural, Torres Vedras, Portugal; USNM, United States National Museum, Washington, DC, USA; YPM: Yale Peabody Museum, New Haven, CT, USA.

12.4. GEOLOGICAL SETTINGS

SHN 181 was found in sediments outcropping at the cliffs north of Valmitão (Lourinhã, Fig. 12.1a), south of the type locality of *Dinheirosaurus lourinhanensis* (Dantas et al., 1992). The sedimentary sequence outcropping in the north sector of Valmitão fits in the Upper Jurassic to Lower Cretaceous sequence deposited in the Lusitanian Basin during the third rifting episode (Rasmussen et al., 1998; Kullberg et al., 2006), a period marked by the internal differentiation of the basin into several sub-basins and resulting in an important siliciclastic input that progressively infilled these basins (Pena dos Reis et al., 2000). After the Kimmeridgian, the sedimentary sequence is strongly siliciclastic with a continental signature at the top of the sequence (Hill, 1988).

The cliffs north of Valmitão are located in the Bombarral Sub-basin (Guéry, 1984), or Consolação Sub-basin (following Taylor et al., 2013), and the outcropping sediments belongs to the Praia da Amoreira-Porto Novo Formation, dated as upper Kimmeridgian-to-basal Tithonian in age (Fig. 12.1b, Manuppella et al., 1999). All remains were found in association and come from laminar black-to-gray mudstones intercalated in fine sandstones rich in plant remains. SHN 181 includes anterior caudal vertebrae, chevrons, and scapular, pelvic and hindlimb elements. The Praia da Amoreira-Porto Novo Formation sediments correspond to aluvial and meandriform fluvial environments and yield a rich vertebrate fossil record (Lapparent and Zbyszewski, 1957; Dantas, 1990; Manuppella et al., 1999; Antunes and Mateus, 2003; Ortega et al., 2009). Dinosaur faunas are represent by theropods: *Ceratosaurus* (Mateus and Antunes, 2000; Malafaia et al., 2015); *Torvosaurus gurneyi* (Hendrickx and Mateus, 2014) and *Lourinhanosaurus antunesi*

(Mateus, 1998); sauropods: *Dinheirosaurus lourinhanensis* (Bonaparte and Mateus, 1999) and *Zby atlanticus* (Mateus et al., 2014); and stegosaurids: *Dacentrurus armatus* (Antunes and Mateus, 2003; Escaso, 2014).

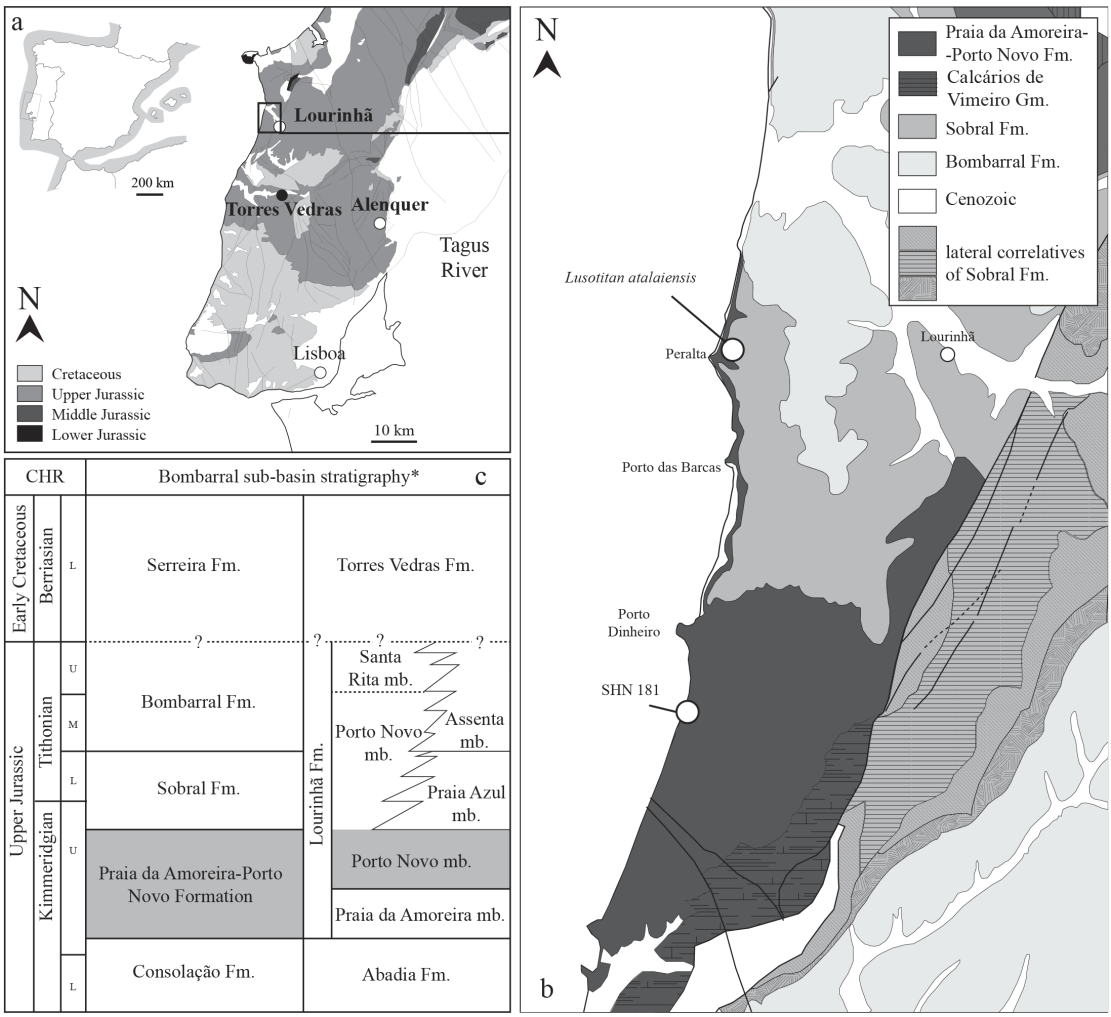


Figure 12.1. a) Geological map (adapted from Oliveira et al., 1992) showing the Portuguese Mesozoic levels; b) Geological map of the Lourinhã region (adapted from Manuppella et al., 1999) with the location of the SHN 181 site in Valmitão; c) Stratigraphy of Bombarral Sub-basin *sensu* Manuppella et al. (1999) and Hill (1988), CHR – Chronostratigraphy.

12.5. SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842
Saurischia Seeley, 1887
Sauropodomorpha Huene, 1932
Sauropoda Marsh, 1878
Macronaria Wilson and Sereno, 1998
Camarasauromorpha Salgado et al., 1997
Camarasauromorpha gen. et sp. nov

Material: A single individual (SHN 181) with eight anterior caudal vertebrae (SHN 181/001-008) preserving several neural arches (SHN 181/000 and 009-019), an anterior chevron and a chevron fragment (SHN 181/020-021), right scapula (SHN 181/022) and coracoid (SHN 181/023), postacetabular process of a left ilium (SHN 181/024-025), two ischia (SHN 181/026-027), two pubis (SHN 181/028-029), a right femur (SHN 181/30), a right tibia (SHN 181/31), a right fibula (SHN 181/32) and a right astragalus (SHN 181/33).

Horizon and locality: The specimen SHN 181 was found in the cliffs of Valmitão in the municipality of Lourinhã (Lisboa, Portugal), Praia de Amoreira-Porto Novo Formation, upper Kimmeridgian-basal Tithonian in age (Manuppella et al., 1999).

12.5.1. Description

Anterior caudal vertebrae: Eight anterior caudal centra (SHN 181/001-008) and several neural arch fragments (SHN181/009-019 and SHN 181/000) are preserved and all of them are affected by an important transverse deformation (Figs. 12.2-12.5). The anterior articular facet of the anteriormost centrum is concave and the posterior one is flat. In the two subsequent centra, the dorsal area of the posterior articulation becomes smoothly concave. Posteriorly, along the caudal series, the posterior articulation becomes progressively concave, and centra become amphicoelous. The posterior articulation remains concave up to the last preserved centra, that following Tschopp et al. (2015) is considered herein one of the last anterior caudal vertebrae (since still preserves a caudal rib). The original transverse outline of the centrum is difficult to recognize due the deformation, but in the less deformed centrum, seems to be subcircular (Figs. 12.2, 12.3; the transverse width is higher in the most proximal caudal vertebrae probably due the deformation). The less deformed centra (CdE and CdF) have a subcircular outline, slightly compressed transversely. The ventral face is generally flat, sometimes slightly concave near the articulations for the chevrons due the presence of two longitudinal ridges associated to these articulations. This concavity is different from the ventral concavity present in diplodocids or saltasaurids (e.g. Tschopp et al., 2015), that are deeper and delimited by well-developed ventrolateral crests along the anteroposterior width of the ventral face. These facets are semicircular and located in anterior and posterior rim of the centrum. The posterior ones become progressively more pronounced and bigger along the tail and from the CdF they bear a concave surface.

Caudal ribs are dorsoventrally compressed with a rounded end in dorsal view. They are posterolaterally projected reaching and surpassing in some cases the posterior edge of the centrum (CdB, C, E, and F). The distal tip of the caudal ribs expands slightly anteroposteriorly and is not posteriorly deflected as occur in *Tastavinsaurus* (Canudo et al., 2008; Royo-Torres, 2009). The distal tip of the caudal ribs bears a ventral deflection resulting in an arched profile in anterior/posterior view as occur in some specimens of *Camarasaurus* (e.g. McIntosh et al., 1996b). In anterior caudal vertebrae, the caudal ribs are deep, and extend from the centrum to the neural arch. From the anterior margin of the ribs of most anterior caudal vertebrae parts a rough lamina, interpreted herein as a incipient prdl that goes toward the prezygapophyses process. The cprf is smooth and undeveloped. The neural channel is dorsoventrally high and lacks a ventral excavation as occur in *Spinophorosaurus* or in a partial tail from Batalha (MG 4974) so far unpublished (pers. observ., PM). The neural arches are totally fused, and the lateral face of the neural arch bears several rugosities. The neural arches are slightly displaced anteriorly but never reach the anterior edge of the centrum. Prezygapophyses are anterodorsally projected with the articular facets facing dorsomedially, and surpassing the anterior margin of the centrum. The medial side of the prezygapophyses surface deflects ventrally resulting in an accessory articulation, which faces medially (Fig. 12.5), considered herein as a possible autapomorphy of SHN 181. Ventral to this accessory articulation there are an associated groove.

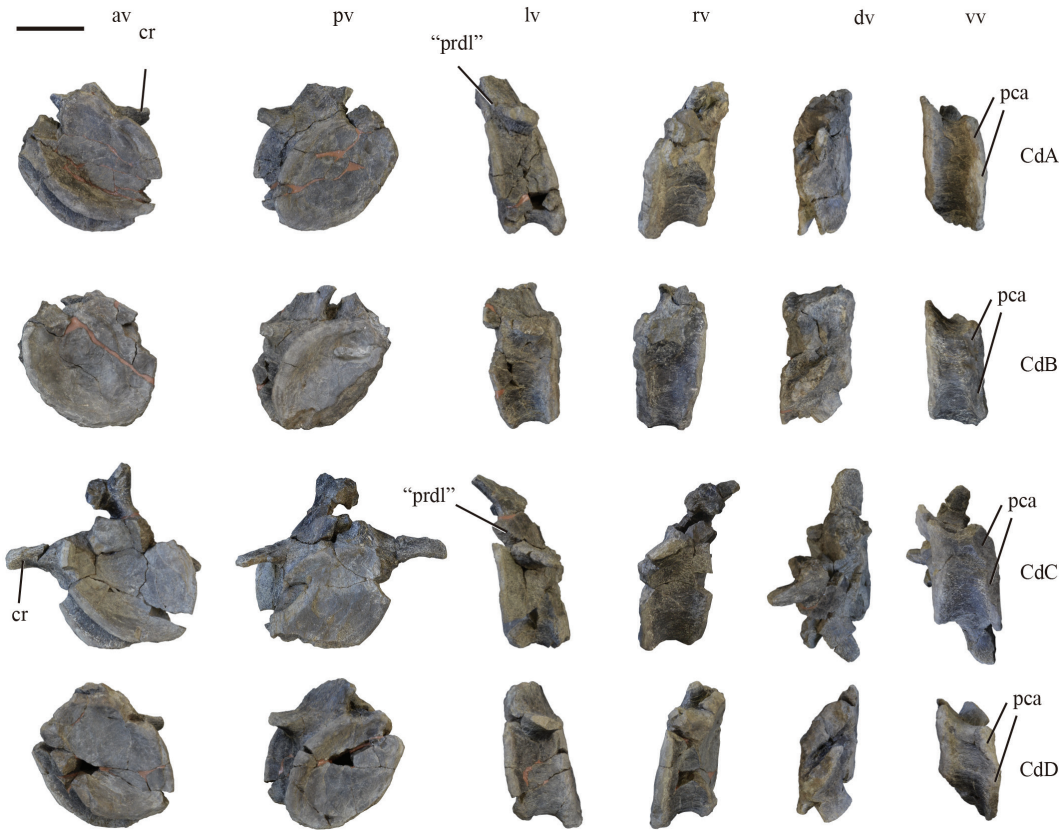


Figure 12.2. Anterior caudal vertebrae (SHN 181/1-4, CdA-CdD) in anterior (av, 1st column), posterior (pv, 2nd column), left (lv, 3rd column), right (rv, 4th column), dorsal (dv, 5th column) and ventral (vv, 6th column) views. Scale bar: 10cm

Several fragments of anterior caudal neural spines were recovered (Fig. 12.4, SHN 181/009-019). All preserved caudal spines are transversely compressed and slightly expanded distally. This expansion is more pronounced in the most proximal ones. The most anterior neural spines have a general posterior deflection. The apex is anteroposteriorly constricted in the most anterior neural spines. The dorsal sector of the posterior face of the neural spine faces dorsoposterioly, and is individualized from rest of the posterior face. In dorsal view, these constricted neural spines have an X-shaped outline. This constriction with this facet is only present in the most proximal anterior neural spines. This combination is proposed as autapomorphy of SHN 181. The dorsal margin of the anteriormost caudal neural spines bears a well-marked longitudinal and sagittal groove, also considered as diagnostic of SHN 181. The anterior and posterior faces of the neural spines bear strongly rough postspinal (posl) and prespinal (prsl) laminae, respectively, being more dorsally pronounced and wide. The prsl becomes transversely constricted and well individualized on the base of the neural spine.

In all apexes of the caudal neural spines, there are lateral depressed and rough areas on the lateral side that is considered an autapomorphy of this sauropod, but shared with *Aragosaurus ischiaticus* (Royo-Torres et al., 2014). In some neural spines this depression is slightly excavated ventrally. On the more posterior preserved caudal neural spines, these lateral

depressions are dorsally connected. The ventral sector of the anterior face is excavated giving place to a dorsoventrally short spinoprezygapophyseal fossa (sprf). This fossa is laterally bordered by spinoprezygapophyseal laminae (sprl). At midheight of the neural spine, sprl become less pronounced and laterally deflected, acquiring a rough morphology. Sprl reach the apex of the spine. The posterior face is also limited by spinopostzygapophyseal laminae (spol), which bear a similar morphology than the sprl. Spol bordered a dorsoventrally short spinopostzygapophyseal fossa (spof). The lateral face of the neural spine bears two dorsoventrally rough ridges behind the sprl and in front of the spol. These two ridges touch each other on the ventral margin of the lateral depressions present dorsally on the neural spine lateral face.

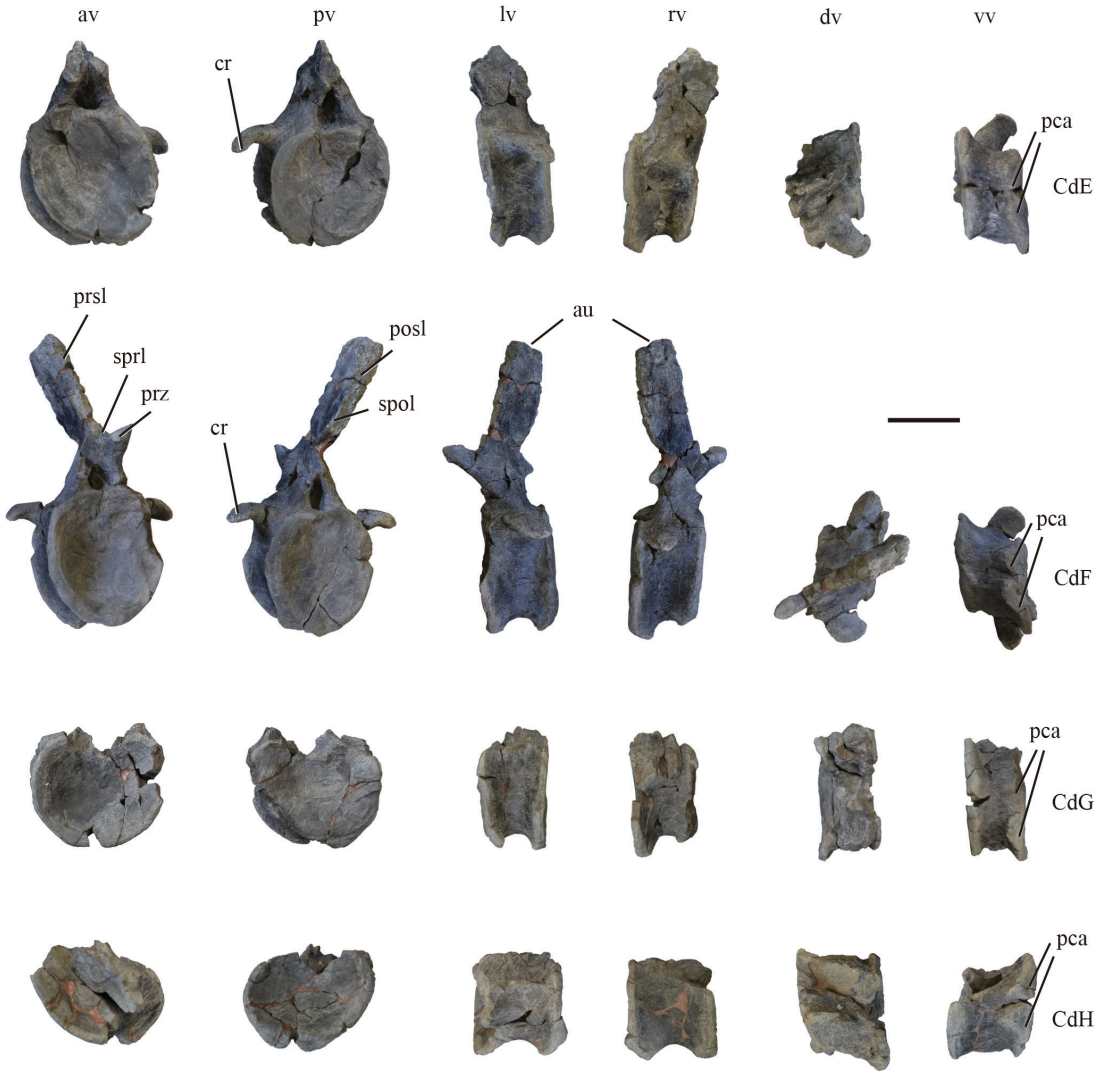


Figure 12.3. Anterior caudal vertebrae (SHN 181/005-008, CdE-CdH), in anterior (av, 1st column), posterior (pv, 2nd column), left (lv, 3rd column), right (rv, 4th column), dorsal (dv, 5th column) and ventral (vv, 6th column) views. Scale bar: 10cm

Figure 12.4. Anterior caudal neural spines (SHN 181/009-010) in anterior (av, 1st line), posterior (pv, 2nd line), right (lv, 3rd line), left (rv, 4th line and dorsal (dv, 5th line). Scale bar: 10cm.

Chevrons: An anterior chevron is preserved (Fig. 12.6, SHN 181/022) and a part of a dorsal branch, including the articulation facet with the caudal vertebrae (SHN 181/021). The articulation facets for the caudal vertebrae are subtriangular in dorsal view, and subdivided into two subfacets, both with a subtriangular outline. The anterior subfacet faces dorsally and is bigger than the posterior one, which faces posterodorsally. These two subfacets are separated by a transversal groove, more pronounced on right articulation (Fig. 12.6b). The lateral border of the articular facet is laterally projected and pointed, deflecting dorsally (Fig. 12.6c-d). The posterior subfacet is bordered by a transverse smooth groove developing ventrally a protuberance. The medial border of the articular

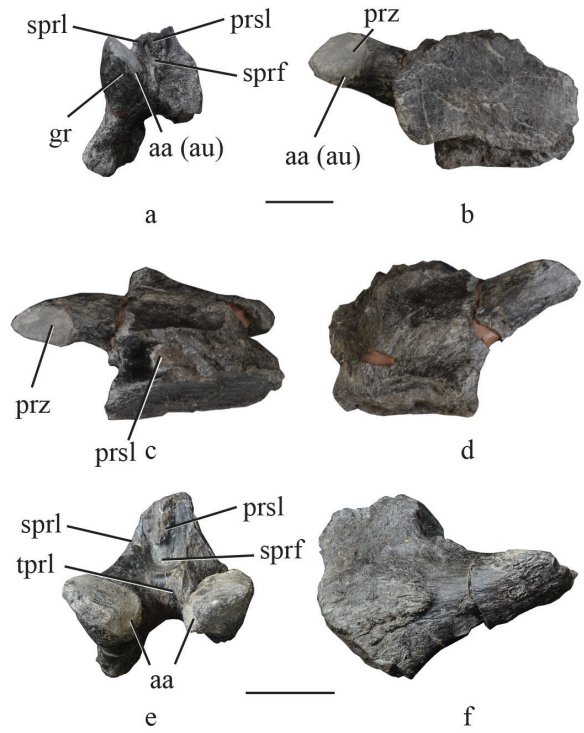


Figure 12.5. Partial anterior caudal neural arches (SHN 181/018-019), in anterior (a, e), left (b), dorsal (c) and right (d, f) views. Scale bar: 3cm.

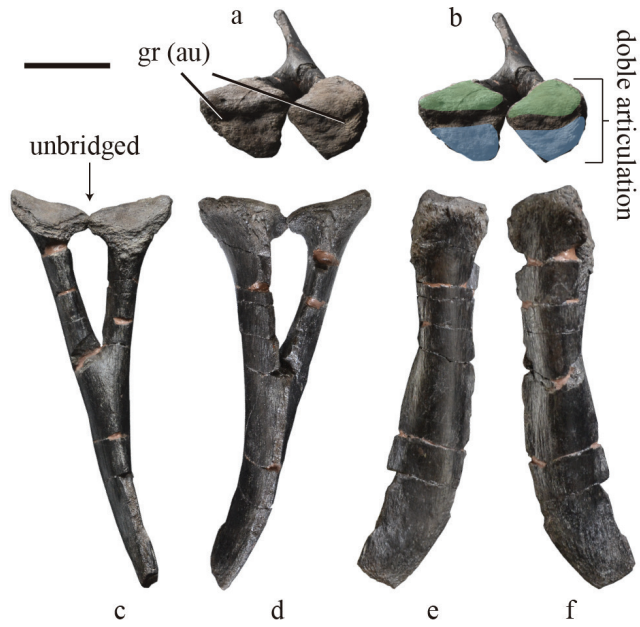


Figure 12.6. Anterior chevron (SHN 181/020) in dorsal (a, b), posterior (c), anterior (d), right (e) and left (f) views. Scale bar: 5cm, green and blue colours indicates for the presence of two facets in the chevron heads.

facets is also pointed but no signs of fusion are present, and therefore the chevron is dorsally open. The haemal channel is dorsoventrally short, no more than 35% of the chevron dorsoventral width. The dorsal rami are transversely compressed, as well as, the distal end. This compression becomes more pronounced at the distal end. On the lateral face of the distal end, near the posterior and the anterior borders, there are several rugosities. On the posterior face of the distal end, just below the haemal channel, there is a longitudinal crest. This crest seems to be present on the anterior face, but this area is poorly preserved. In lateral view, the distal end is posteriorly deflected.

Scapula: A right scapula lacks the dorsal margin of the scapular blade and the acromial process (Fig. 12.7, SHN 181/022). In ventral/dorsal view, the scapula shows a general curvature with the convexity facing laterally. Laterally, the acromial process develops an acromial fossa. This fossa is posteriorly limited by an acromial ridge as pronounced as in *Camarasaurus grandis* or *Brontosaurus excelsus* (Ostrom and McIntosh, 1966). The region of the glenoid is mediolateral expanded and thick. The glenoid surface is rough and concave facing mainly anteriorly. The lateral surface of the scapula bears several rugosities, including a rough area near the glenoid, unusual for sauropods. On the medial side of the scapula there are a circular rough tuberosity, but not so pronounced than the tuberosity present on the medial face of acromial process in *Saltasaurus* (Powell, 1992). The presence of this tuberosity on the medial face of the scapula is considered as an autapomorphy of SHN 181.

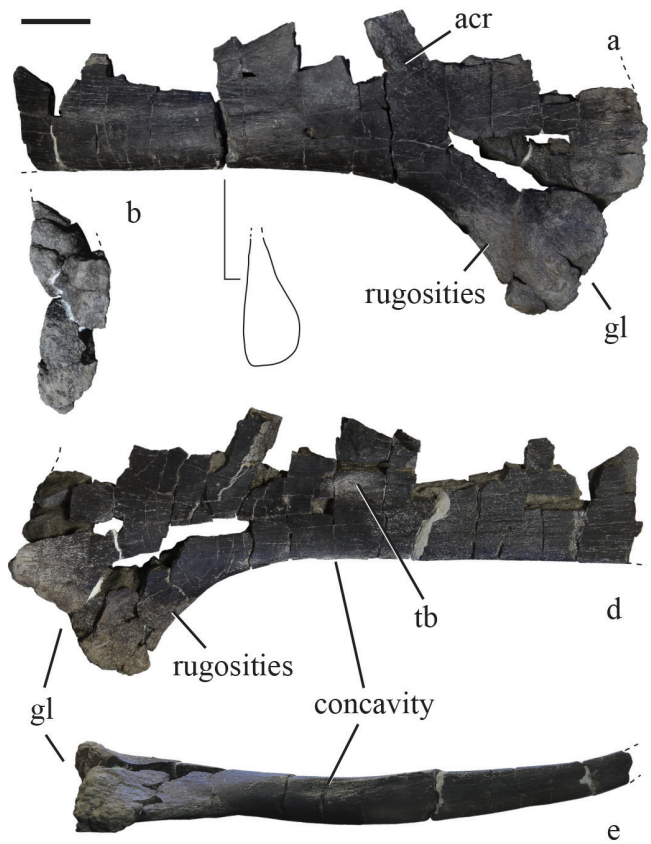


Figure 12.7. Partial right scapula (SHN 181/022) in lateral (a), proximal (b), medial (d) and ventral (e) views, and cross-section of the scapular blade (c). Scale bar: 10cm. Traced line: broken borders.

The scapular blade has a transversely convex lateral face and a flat medial face, resulting in a well-defined D-shaped cross-section. The scapula blade becomes thinner distally. The preserved sector of the scapula does not allow testing the presence of a distal expansion as occur in other sauropods such as rebbachisaurids or camarasaurids (Osborn and Mook, 1921; Ostrom and McIntosh, 1966; Salgado et al., 2004). At the base of the scapula blade, on the ventral surface, there is an elliptical concavity considered as an autapomorphy of SHN 181. Medially to this concavity starts a ventral sharp crest that fade away at midpoint of the scapula blade preserved length.

Coracoids: Incomplete right coracoid lacking the dorsal half is preserved (Fig. 12.8, SHN 181/023). The preserved section of the coracoid does not allow us to observe several important features related with its dorsal margin and the general morphology of this element. The glenoid is thick transversely and concave bearing an oval format. The coracoid foramen is presented and bears an elliptical outline with the maximum diameter anteroventrally-posteromedially oriented. The coracoid foramen perforates with a medioposterior direction and is totally close. The lateral face of the coracoid is mainly flat and the posterior one concave. The medial and lateral surface of the coracoids bears several rugosities on the surface. The preserved sector of the anterior border of the coracoid is smoothly round. The scapula and the coracoid are in contact but it is not possible to confirm that they are fused.

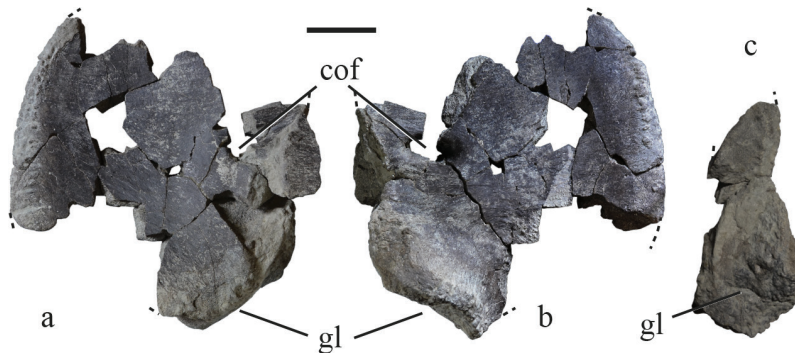


Figure 12.8. Partial right coracoid (SHN 181/023) in medial (a) and lateral (b) views. Scale bar: 10 cm. Traced line: broken borders.

Ilium: Only the postacetabular process (poap) of the left ilium (SHN 181/024) and an isolated fragment of the iliac blade dorsal margin (SHN 181/025) are preserved in SHN 181 (Fig. 12.9). The poap bears a triangular profile, dorsoventrally constricted. On the ventral margin, close to the distal end of the poap, there is a hook-shaped tuberosity. Anterior to this tuberosity, the ventral margin of the poap is acute. The medial surface of the postacetabular process is concave up to the posteriormost sacral rib facet.

The preserved dorsal margin of the ilium becomes thicker up to the last sacral rib resulting in a thick and rough rim on the dorsal margin of the ilium and medially located. Two dorsoventral ridges are preserved in the medial side of the ilium and another one in the isolated fragment. These ridges mark the attachment between the iliac blade and the transverse processes of the sacral vertebrae.

The lateral surface is slightly convex anteroposteriorly, and close to the dorsal edge, the surface becomes rough and several rugosities are present. This dorsal rough area is delimited by a coarse ridge, more pronounced at the level of the sacral ribs facets. A triangular process extends ventrally from this rough area close to the distal tip.

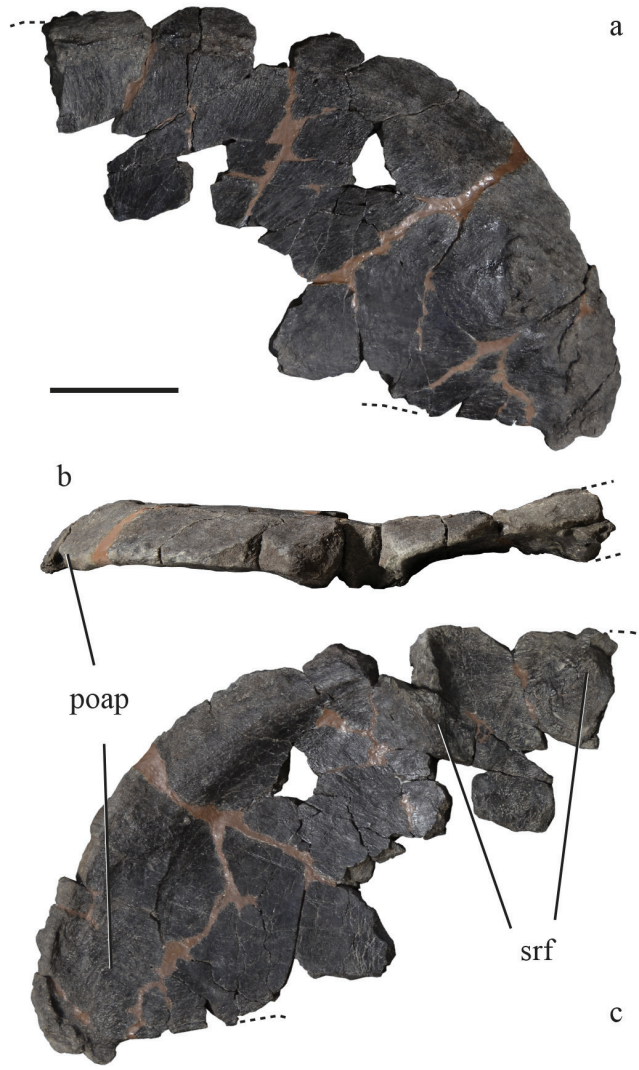


Figure 12.9. Postacetabular process of the left ilium (SHN 181/024) in lateral (a), dorsal (b) and medial (c) views. Scale bar: 10cm. Traced line: broken borders.

Ischia: Two partial ischia are preserved (SHN 181/026-027), but in any of them is possible to observe a complete proximal plate (or pubic peduncle) and acetabulum (Figs. 12.10, 12.11). The left ischium also lacks the iliac peduncle. The ischia are shorter than the pubis (the pubis is 116% of the ischium, Fig. 12.12). The iliac peduncle is elliptical in dorsal view, and the anterior part of its lateral border is laterally projected. The surface is rough and slightly concave. On the lateral face, near the dorsal margin of the ischiatic peduncle there are a well-developed tuberosity. This tuberosity appears in the transition of the ischiatic peduncle and the proximal plate. Despite the presence of a smooth concavity, anterodorsally located from this tuberosity, this structure is not bordered by a groove as occur in *Dicraeosaurus* (Janensch, 1961), *Lourinhasaurus* (Mocho et al., 2014a), *Camarasaurus* (Ostrom and McIntosh, 1966), *Aragosaurus* (pers. observ., PM) or *Spinophorosaurus* (pers. observ. PM). The tuberosity is not observable in medial view as occur in some titanosaurs. The ischiatic peduncle has a teardrop-shaped cross-section with an acute medial

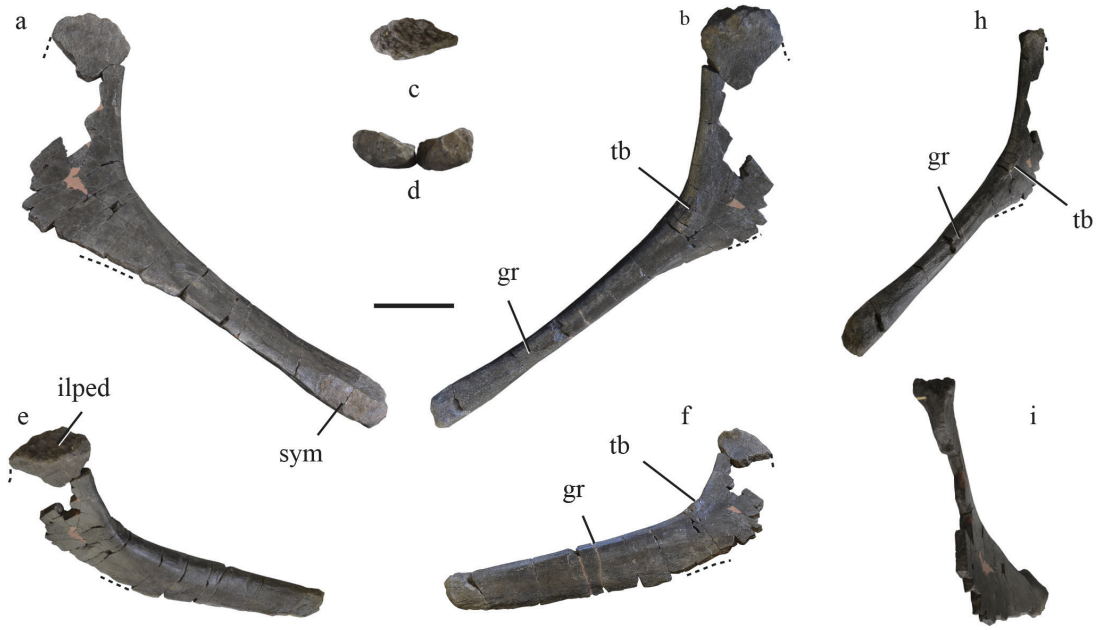


Figure 12.10. Right ischium (SHN 181/026) in medial (a), lateral (b), dorsal (e), ventral (f), posterior (h) and anterior (i) views. Iliac peduncle of the right ischium in proximal view (c). Ischiatic peduncles of right and left ischia in distal view (d). Scale bar: 10 cm

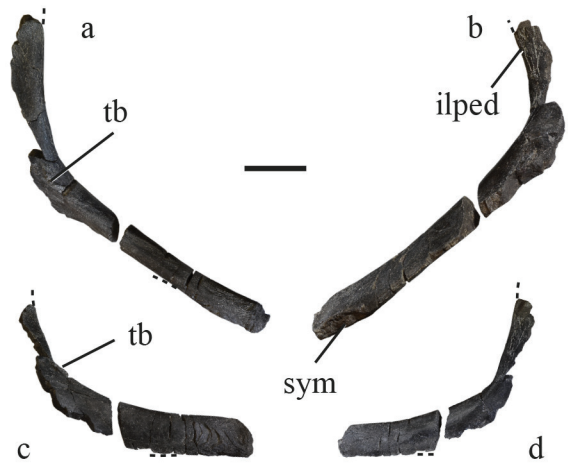


Figure 12.11. Left ischium (SHN 181/027) in lateral (a), medial (b), dorsal (e) and ventral (f) views. Scale bar: 10 cm. Traced line: broken borders.

margin becoming semi-elliptical distally and with a flat medial surface. It twists along its length becoming coplanar in the distal end. The medial margin of the distal end is thicker and bears a teardrop-shaped rough facet, anteroposteriorly elongated, that corresponds to the symphyses between ischia. The distal end is rough and not expanded. The maximum diameter of the distal end is twice the minimum one, resulting in a transversely short distal end that is considered an autapomoporphy of SHN 181. Ventrally to the lateral tuberosity of the ischiatic blade, on the lateral side and near the ventral border of the ischiatic blade a longitudinal smooth concavity is present.

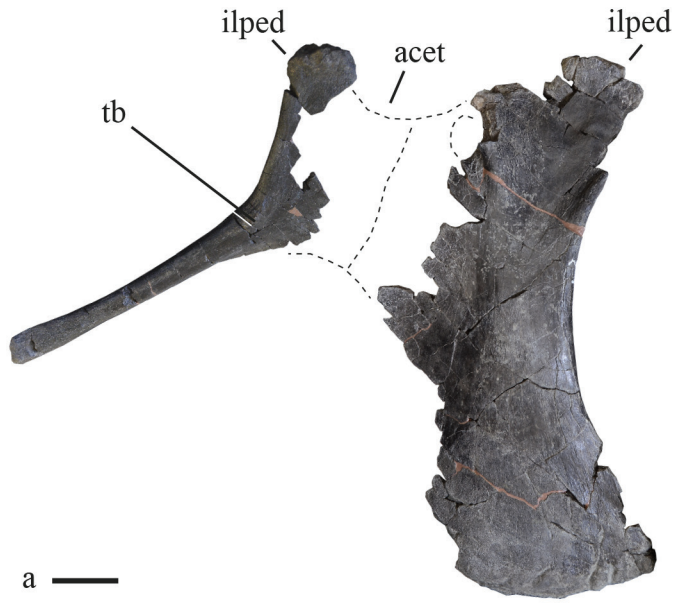


Figure 12.12. Right ischium (SHN 181/026) and pubis (SHN 181/028) in lateral view (a). Sacle bar: 10cm. Traced line: broken borders.

Pubis: Two partial left and right pubis was recovered (Fig. 12.13, SHN 181/028-029). In the right pubis, the posterior section of the ischiatic peduncle is not preserved, but in the left one, part of the distal end of the pubic articulation was recovered. Pubis of SHN 181 are longer than the ischia (the pubis is 116% of the ischium, Fig. 12.12). The iliac peduncle (ilped) is transversely compressed (although it may be slightly). In dorsal view, the ilped shows an elliptical outline with the maximum diameter anteroposteriorly oriented. The proximal surface of the ilped is rough and slightly concave. The lateral surface of the ilped bears a triangular fossa and the medial side is anteroposteriorly convex. The ilped is dorsoventrally short as occur in *Lusotitan*.

Just below the acetabulum, it is preserved part of the obturator foramen piercing the ischiatic peduncle with a lateroventral-to-dorsomedial orientation. The anterior border of the obturator foramen is well developed, resulting in a ridge-like structure. On the left pubis, the ventral end of ischiatic articulation becomes thinner and deflects medially in the transition with the symphysis, resulting in an S-shaped symphysis in posterior view. In the left pubis the posteriormost region of the acetabulum is preserved being possible to estimate that the ischiatic articulation corresponds to 50% of the total length of the ischium. The medial surface of the ischiatic peduncle is generally depressed. The acetabulum is well preserved in the left pubis, its surface is rough and concave dorsoventrally, being bordered ventrally by a ridge.

The medial face of the pubic peduncle is flat and the anterior margin is concave in medial/lateral view. The anterior margin is also round transversely but becomes transversely compressed on the distal end resulting in a coarse, acute border and laterally projected. In the medioventral border of the distal end, it is preserved part of the symphysis that has a semi-elliptical outline. The distal end is anteroposteriorly expanded and the distal surface is rough, concave and elliptical in distal view.

Femur: An almost complete right femur is preserved but lacking a portion of shaft (Fig. 12.14, SHN 181/030). The femur has a straight profile in anterior and lateral views. The fourth trochanter is located at midline of the posterior face of the shaft and it is robust as in basal eusauropods (Remes

Figure 12.13. Right (SHN 181/028) and left (SHN 181/029) pubis in dorsal of the (a, g), ventral (b, h), lateral (c, i), anterior (d, j), medial (e, k) and posterior (f, l) views. Scale bar: 10cm. Traced line: broken borders.

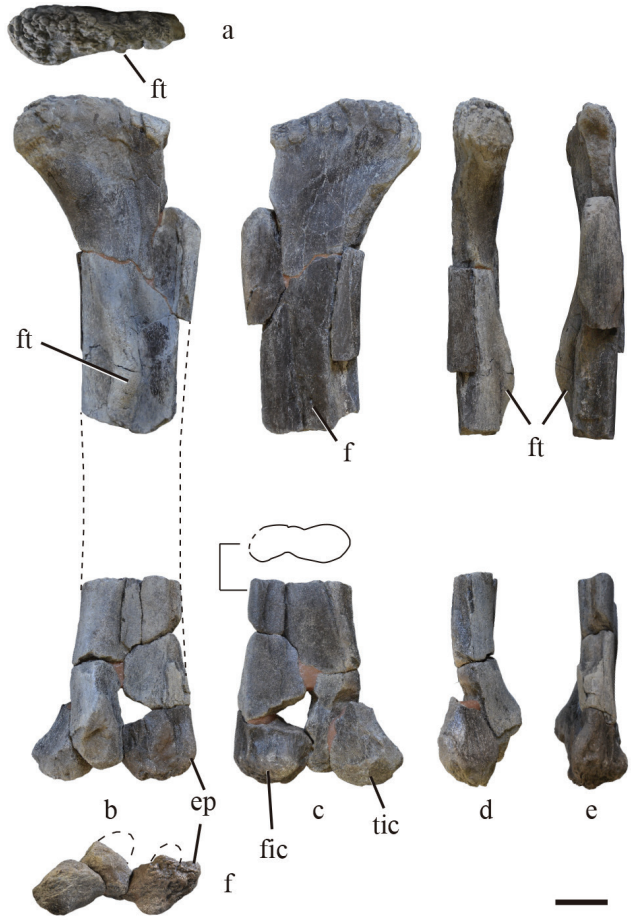


Figure 12.14. Right femur (SHN 181/030) in proximal (a), posterior (b), anterior (c, including the cross-section of the femur diaphysis), medial (d), lateral (e) and distal (f) views. Scale bar: 10 cm, Traced line: missing bone.

et al., 2009), but round and asymmetrical (although some erosion might be present) in lateral view. In posterior view, the fourth trochanter bears an arched outline, with the convexity facing laterally. Medially to the fourth trochanter, the surface of the diaphysis has a rough tuberosity. Dorsal to this tuberosity there is a small concavity. On the anterior face, at the level of the fourth trochanter ventral tip, the shaft is pierced by small foramina. Close to the dorsolateral edge of the femur, the lateral edge becomes thicker and acquired a rough surface. The femoral head is compressed anteroposteriorly and slightly dorsomedially projected. Besides the absence of the laterodorsal corner of the femur, the absence of a pronounced lateral bulge and medial deflection can be interpreted. Nevertheless, is not excluded the presence of a dorsoventral short lateral bulge as occur in *Tastavinsaurus* (Royo-Torres, 2009). In SHN 181 the shelf trochanter and the *linea intermuscularis cranialis* are absent. The preserved sector of the shaft is anteroposteriorly compressed, resulting in a sub-elliptical outline. The tibial and fibular condyles are beveled anteromedially-to-posterolaterally (probably due to deformation). The tibial condyle is bigger than the fibular one. The tibial and fibular condyles are slightly extended to the anterior face of the femur. The epicondyle is well developed and separated from the fibular condyle by a well-defined proximodistal groove.

Tibia: The right tibia is complete (Fig. 12.15, SHN 181/031). The tibia is straight along all its length. The proximal section is transversely compressed, probably due to deformation. In the lateral face of the proximal end, there are a triangular scar for the articulation of the fibula. When the fibula is articulated with the tibia, the posterior half of the lateral surface of the proximal end is uncovered. It is difficult to interpret functionally this condition and probably is due to a significant deformation. Perhaps, this region originally faced posteriorly, and so, the most reliable outline for the proximal end, is a subcircular outline (this feature is scored as unknown in the data matrix). The fibular articulation is rough and bordered posterior by a thick, rough and lateral projected cnemial crest. This crest does not have a triangular profile as occur in *Lusotitan* (Mannion et al., 2013) or in *Apatosaurus* (Gilmore, 1936). The proximal surface bears pronounced rugosities, is flat posteriorly and concave anteriorly. Near the lateral edge, and above the fibular articulation, the proximal surface bears a boss. In this tibia there are not signs of a 2nd cnemial crest *sensu* Bonaparte et al. (2000) and Mannion et al. (2013). The diaphysis is also transversely compressed, probably due to taphonomical compression, bearing an oval outline in cross-section (the maximum diameter is anteroposteriorly oriented). The distal end represents the less deformed region of the tibia, but the articular surface for the ascending process (aspa) is broken, lacking its distal tip. Despite the presence of a partial aspa, it is possible to conclude that the distal section of the tibia has a sub-circular outline. The distal end is not transversely expanded. The aspa has a flat surface, occupying a dorsal position respect to posterior ventral process (pvp). As in *Lusotitan* (Mannion et al., 2013), the aspa and pvp are laterally separated from the distal surface by a groove that does not progress to the lateral face of the distal end. The pvp is oval and smaller than aspa and has a convex and rough surface. The medial face of the distal end bears an oval bulge.

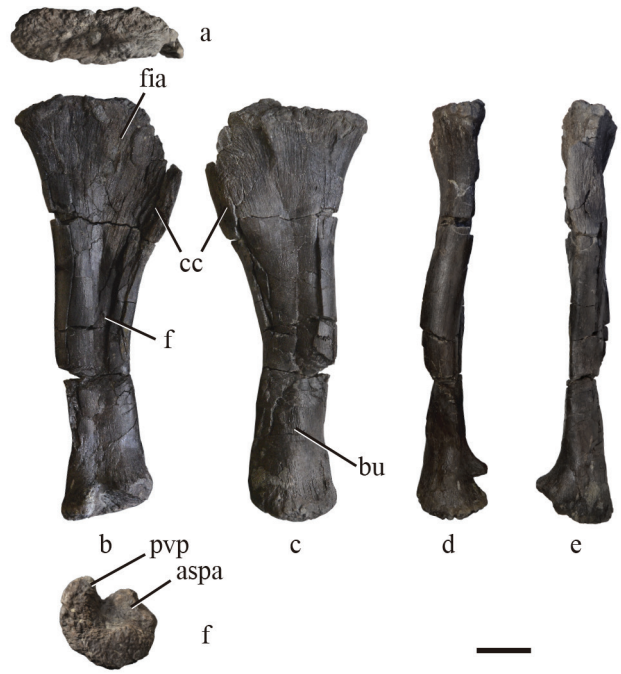


Figure 12.15. Right tibia (SHN 181/031) in proximal (a), posterior (b), lateral (c), ventral (d), anterior (e) and distal (f) views. Scale bar: 10 cm.

Fibula: A complete right fibula is preserved presenting a slight transverse compression in the distal end (Fig. 12.16, SHN 181/032). The fibula shows a pronounced sigmoid profile as in other sauropods such as *Tastavinsaurus* or some specimens of *Camarasaurus* (Ikejiri, 2004; Canudo et

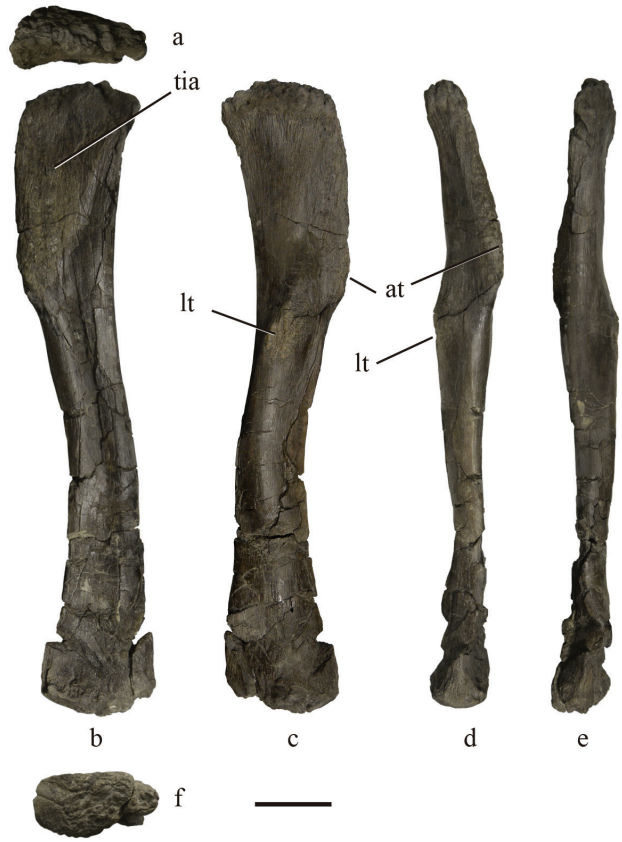


Figure 12.16. Right fibula (SHN 181/032) proximal (a), medial (b), lateral (c), anterior (d), posterior (e) and distal (f) views. Scale bar: 10 cm.

al., 2008; Royo-Torres, 2009) resulting from the deflection of the proximal end. Below the anterior trochanter, there is a marked shoulder, at level of the end of the tibial scar. The proximal third of the fibula is expanded having a subrectangular profile in lateral/medial view. The proximal end expands at the level where appears the tibial scar), The posteroproximal edge is slightly pointed. The tibial articulation is striated, well developed and has a long proximodistal triangular outline, occupying the proximal third of the fibula. The anterior margin of the proximal end is thicker, especially near the ventral tip of the tibial scar. In this area is located the anterior trochanter and also a shoulder that results from the deflection of the proximal end. This trochanter is not a well-developed crest as in somphospondylians (D'Emic, 2012). In the proximalmost part of the anterior margin of the fibula there is a proximodistal sulcus. The lateral surface of the anterior trochanter is not anteroposteriorly concave, unlike the marked concavity present in *Tastavisaurus* (Royo-Torres, 2009) and some somphospondylians (Martin, 1999). The medial face of the diaphysis is transversely concave-to-flat, resulting in a D-shaped cross-section. The general morphology of the lateral trochanter is oval with a rough surface; however, this oval trochanter is composed by three rugosities not well individualized. The region of the lateral trochanter is posteriorly projected producing a marked shoulder in the lateral face of the tibia, well visible in anterior/posterior view, as occur in titanosaurs (Powell, 2003; Otero, 2010). The proximal edge is convex in lateral view. The proximal surface has a transversely compressed subrectangular outline, and bears pronounced rugosities, that extends to the medial and lateral face of the proximal end. The medial edge of the distal section is projected, forming a medial lip, which articulates with the astragalus, as occur in

some sauropods such as *Lourinhasaurus* (Mocho et al., 2014a). The distal surface is rough and flat-to-concave and bears a semicircular-to-oval outline (straight medial edge) as in several other sauropods (Royo-Torres, 2009). The rough distal surface extends to the lateral and the medial faces of the fibula.

Astragalus: A complete right astragalus was found (Fig. 12.17, SHN 181/033). This astragalus bears an oblique deformation and compression, being impossible the articulation with the correspondent tibia. Furthermore, when the both elements are partially articulated, the medial apex of the astragalus surpasses the medial face of the tibial distal end. We considered that this is due to a significant proximodistal compression in the astragalus. All the surface of astragalus, excluding the articulation surface for the fibula, bears marked rugosities. The astragalus is wedge-shaped, and in proximal view, it becomes narrow anteroposteriorly. Also in proximal view, the anterior edge is transversely straight-to-convex. The posterior edge of astragalus is straight, transversely oriented behind the ascending process, but the medial sector deflects posteriorly with a concave profile, culminating in a pointed apex of astragalus. In anterior view, the apex of the astragalus is proximodistally constricted. The ascending process almost reaches the posterior margin of astragalus (when the dorsal surface of the ascending process is in horizontal). Its proximal surface is flat and rough. The posterior surface of the ascending process is markedly separated from the proximoposterior surface of the medial part of the astragalus. The surface is deep, bearing two main foramina separated by subvertical ridge. The medial foramen is divided in a main anterior subfossa and a posterior small one. The posterodistal edge of the astragalus, just ventrally to the ascending process, is proximally projected resulting in a pronounced tongue-like structure. This proximal projection is particularly uncommon in the astragalus of sauropods but the degree of compression in this specimen does not allow considering this feature as a reliable autapomorphy. New material is needed to test the permanence of this condition so unusual. The proximal surface of the medial tip of the astragalus is broadly concave, smoother than the rest of astragalus surface, and bears a posterior slope. The rough ventral face of astragalus is transversely convex and transits continuously to the also rough anterior face. The ventral surface bears a circular and smooth concavity, at ascending process level. Just below the anterior margin of the ascending process, there is a transverse groove on the anterior surface of the astragalus. The articular surface for the fibula faces laterally, is well limited, and occupies the dorsal part of the lateral surface of astragalus.

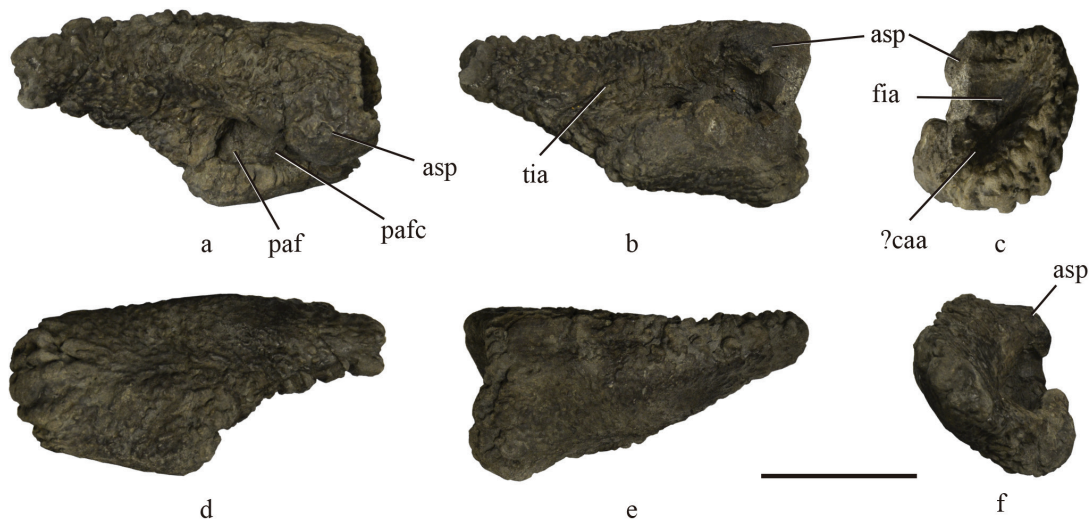


Figure 12.17. Right astragalus (SHN 181/033) in medial (a), lateral (b), anterior (d) and proximal (e) views, and the cross section outline of the fibula diaphysis (c).

12.6. PHYLOGENY

The phylogenetic analysis for SHN 181 was performed using the data matrix proposed by Carballido and Sander (2014). The data matrix was analyzed using TNT 1.1 (Goloboff et al., 2003) to find the most parsimonious trees (MPTs). We used a heuristic tree search performing 1000 replications of Wagner trees (using random addition sequences) followed by tree bisection reconnection (TBR) as swapping algorithm, saving 10 trees per replicate. To test the support of the phylogenetic hypotheses, Bremer support and bootstrap (absolute frequencies based on 5000 replicates) values were performed in TNT 1.1. (Goloboff et al., 2003).

As in the original analysis (Carballido and Sander, 2014), the multistate characters 12, 58, 95, 96, 102, 106, 108, 115, 116, 119, 120, 154, 164, 213, 216, 232, 233, 234, 235, 256, 267, 298, 299 and 301 were considered ordered. The result of this analysis yielded 48 MPTs of 999 steps with a consistency index (CI) of 0.405 and a retention index (RI) of 0.733 (Fig. 12.18). The general topology obtained is similar to that proposed by Carballido and Sander (2014), but with an significant polytomy at the base of Camarasauromorpha including *Europasaurus*, *Galveosaurus*, *Bellusaurus*, *Euhelopus*, *Tastavinsaurus*, *Tehuelchesaurus*, *Camarasaurus*, SHN 181, *Chubutisaurus*, *Brachiosaurus*, *Giraffatitan*, *Paluxysaurus*, *Venenosaurus*, *Cedarosaurus*, *Erketu* and ((*Wintonotitan* + *Tendaguria*) + and more derived titanosauriforms) (see Fig. 12.18).

In this phylogenetic hypothesis, Camarasauromorpha is supported by 15 synapomorphies. Nevertheless, is important to taking into account the poor resolution present at the base of Camarasauromorpha, where is included the specimen described herein.

SHN 181 is placed within Camarasauromorpha by the presence of procoelous/distoplatyan caudal vertebrae (character 193), and fibular facet of the astragalus facing laterally (character 317). Despite the absence of the puboischial contact, on the left pubis, the ventral part of this contact is preserved and it is predictable to expect that the puboischiatic contact correspond to 40% of the total length of the pubis of SHN 181. This character was scored as unknown for SHN 181, but can be inferred the presence of the derived condition.

The incompleteness of the type material of SHN 181 is probably responsible of part of the low resolution at the base of Camarasauromorpha. Furthermore, *Tehuelchesaurus* is a taxon with many plesiomorphies recovered as a non-neosauropod eusauropod in some phylogenetic approaches (e.g. Upchurch et al., 2004), and *Galveosaurus* is also composed by a significantly incomplete specimen (Royo-Torres et al., 2006, 2009, 2014; Barco, 2009; Carballido et al., 2011; Royo-Torres and Upchurch, 2012; Mannion et al., 2013; Carballido and Sander, 2014).

The result of the analysis recovered for SHN 181 the following autapomorphies: *i*) the transverse width of the anterior caudal neural spines is greater than anteroposterior length (character #198, but present in other taxa in polytomy with SHN 181) and *ii*) fourth trochanter located on the midline of the femoral posterior face (character #308). These features are considered as local autapomorphies of SHN 181 (see discussion).

12.7. DISCUSSION

Despite the fragmentary state of SHN 181, several available features provides significant information in order to discuss the phylogenetic position of this taxon within Eusauropoda. SHN 181 presents an uncommon combination of simplesiomorphies and apomorphies, justifying in part, the establishment as a new taxon.

12.7.1. Non-neosauropod and neosauropod affinities

The presence of a robust fourth trochanter located near the midline of posterior face features the femur of SHN 181. This feature is considered herein as autapomorphy of SHN 181, but it is present in some basal sauropods such as the mamenchisaurids *Mamenchisaurus* (Ouyang and Ye, 2002) and *Omeiasaurus*; *Shunosaurus* (Zhang, 1988); *Patagosaurus* (Bonaparte, 1986); and *Spinophorosaurus* (Remes et al., 2009). The Middle Jurassic sauropod *Bellusaurus* also present this feature (Dong, 1990). *Bellusaurus sui* Dong, 1990 presents an uncertain phylogenetic context, being considered as basal macronarian (Upchurch et al., 2004; Royo-Torres et al., 2006; Carballido and Sander, 2014) or a non-neosauropod eusauropod (Royo-Torres and Upchurch, 2012; Mocho et al., 2014a; Royo-Torres et al., 2014). Nevertheless, this feature is not exclusive for basal eusauropods, being also present in the somphospondylian sauropod, *Euhelopus* (Wiman, 1929; Wilson and Upchurch, 2009).

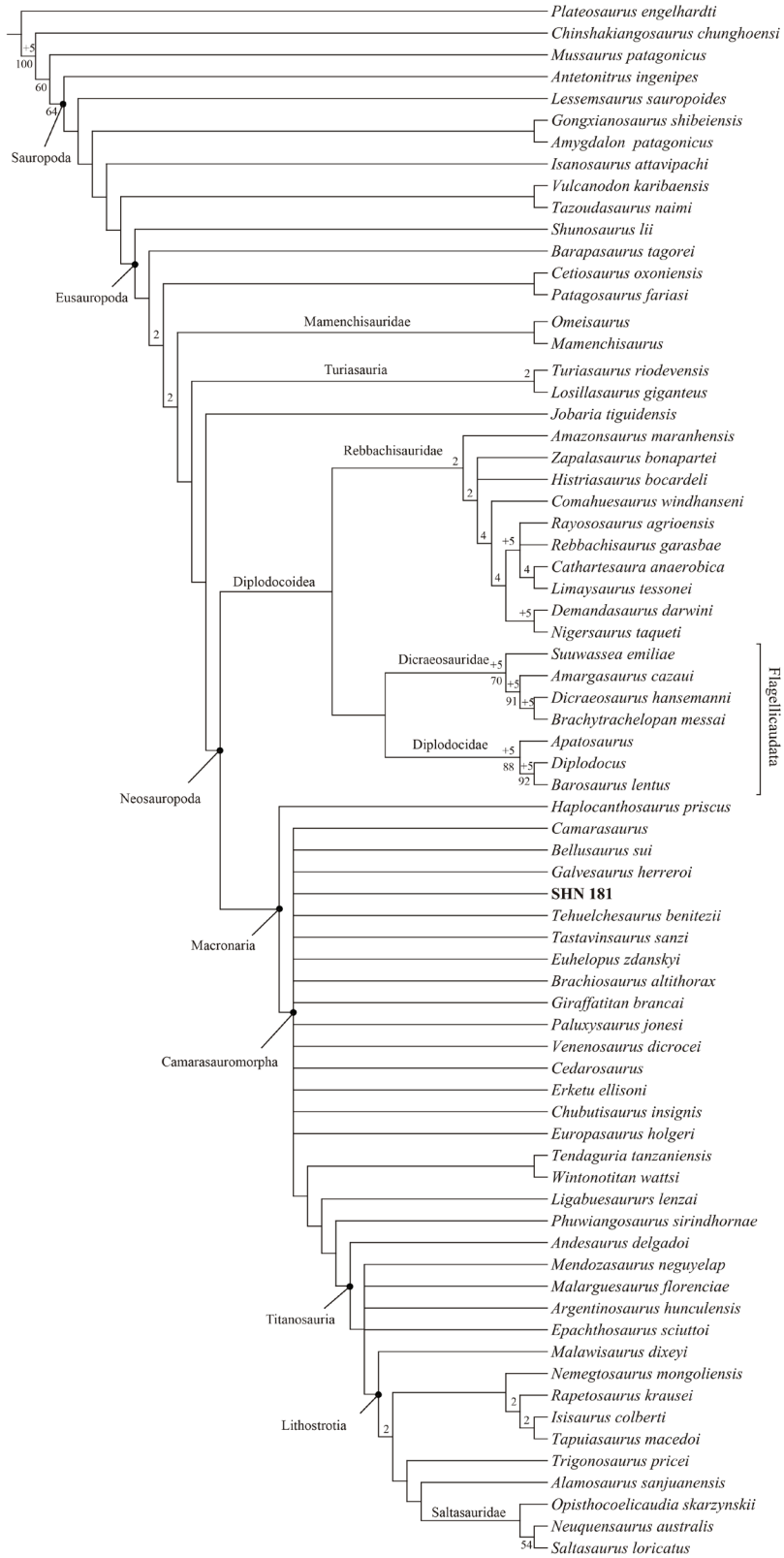
SHN 181 scapula shows several features that are common in neosauropods: (1) a well-developed and pronounced acromial ridge that is not so pronounced in the most basal sauropods as in several Chinese taxa (Upchurch et al., 2004) and in turiasaurs (Royo-Torres et al., 2006; Mateus et al., 2014); and (2) the presence of an excavated area behind the acromial ridge of the scapula (Upchurch et al., 2004). The presence of a D-shaped scapular blade was considered a synapomorphy of *Jobaria* + Neosauropoda (Wilson, 2002) but seems to be a common feature in eusauropods (Carballido et al., 2011) reversing in somphospondylians (Wilson, 2002).

The original morphology of the tibial proximal end is difficult to recognize due to the pronounced deformation. A circular proximal end is considered a synapomorphy of Neosauropoda (Wilson and Sereno, 1998; Wilson, 2002) also present in some derived eusauropod such as *Ferganosaurus*. In SHN 181, we consider that the proximal end probably had a circular outline in life, taking into account the morphology in the articulation between the fibula and tibia. SHN 181 bears an ascending process of astragalus extending to posterior margin of astragalus that was considered a synapomorphy of Neosauropoda (Wilson and Sereno, 1998; Wilson, 2002; Upchurch et al., 2004) or *Mamenchisaurus*+Neosauropoda (Carballido et al., 2011). However, other non-neosauropod eusauropods also presents the derived condition such as *Spinophorosaurus* (pers. observ., PM). The astragalus has a wedge-shaped contour in SHN 181, feature present in neosauropods and derived non-neosauropod eusauropods (e.g. Wilson and Sereno, 1998; Wilson, 2002; Alifanov and Averianov, 2003; Upchurch et al., 2004; Royo-Torres et al., 2006) being recovered as synapomophy of Neosauropoda by Wilson and Sereno (1998) and Carballido et al. (2011) or a synapomorphy of *Jobaria* + Neosauropoda by Wilson (2002).

From the available material of SHN 181 is possible to observe the absence of synapomorphies of Diplodocoidea, one of the most important evolutionary lineages within Neosauropoda (e.g. Upchurch, 1995; Wilson and Sereno, 1998; Wilson, 2002; Upchurch et al., 2004; Harris, 2006; Whithlock, 2011; D'Emic, 2012; Carballido and Sander, 2014), as well as, of Diplodocidae, the only diplodocoid group so far represented in the Iberian Upper Jurassic (Bonaparte and Mateus, 1999; Royo-Torres et al., 2007; Mannion et al., 2012; Mocho et al., 2014b).

12.7.2. Macronarian affinities

Some features suggest the placement of SHN 181 within Macronaria clade. Flat posterior articulation on the most proximal anterior caudal vertebrae present in SHN 181 is shared by basal macronarians (e.g. *Lourinhasaurus*, *Camarasaurus*, *Tastavinsaurus*, and *Giraffatitan*) and is distinct from the procoelous proximal caudal centra of flagellicaudatans and titanosaurs (Salgado et al., 1997; Upchurch et al., 2004; Upchurch and Mannion, 2009) and some non-neosauropods


Plateosaurus engelhardti
Chinshakiangosaurus chunghoensi
Mussaurus patagonicus
Antetonitrus ingenipes
Lessemsaurus sauropoides
Gongxianosaurus shibeiensis
Amygdalon patagonicus
Isanosaurus attavipachi
Vulcanodon karibaensis
Tazoudasaurus naimi
Shunosaurus lii
Barapasaurus tagorei
Cetiosaurus oxoniensis
Patagosaurus fariasi
Omeisaurus
Mamenchisaurus
Turiasaurus riodevensis
Losillasaurus giganteus
Jobaria tiguidensis
Amazonsaurus maranhensis
Zapalasaurus bonapartei
Histriasaurus bocardeli
Comahuesaurus windhanseni
Rayososaurus agrioensis
Rebbachisaurus garasbae
Cathartesaura anaerobica
Limaysaurus tessonei
Demandasaurus darwini
Nigersaurus taqueti
Suuwassea emiliae
Amargasaurus cazaui
Dicraeosaurus hansemanni
Brachytrachelopan messai
Apatosaurus
Diplodocus
Barosaurus lentus
Haplocanthosaurus priscus
Camarasaurus
Bellusaurus sui
Galvesaurus herreroi
SHN 181
Tehuelchesaurus benitezii
Tastavinsaurus sanzi
Euhelopus zdanskyi
Brachiosaurus altithorax
Giraffatitan brancai
Paluxysaurus jonesi
Venenosaurus dicrocei
Cedarosaurus
Erketu ellisoni
Chubutisaurus insignis
Europasaurus holgeri
Tendaguria tanzaniensis
Wintonotitan wattsi
Ligabuesaururs lenzai
Phuwiangosaurus sirindhornae
Andesaurus delgadoi
Mendozasaurus neguyelap
Malarguesaurus florenciae
Argentinosaurus hunculensis
Epachthosaurus sciuttoi
Malawisaurus dixeyi
Nemegtosaurus mongoliensis
Rapetosaurus krausei
Isisaurus colberti
Tapuiasaurus macedoi
Trigonosaurus pricei
Alamosaurus sanjuanensis
Opisthocoelicaudia skarzynskii
Neuquensaurus australis
Saltasaurus loricatus
Sauropoda
Eusauropoda
Mamenchisauridae
Turiasauria
Rebbachisauridae
Diplodocoidea
Dicraeosauridae
Diplodocidae
Neosauropoda
Flagellicaudata
Macronaria
Camarasauromorpha
Titanosauria
Lithostrotia
Saltasauridae

such as *Bellusaurus*, *Chuanjiesaurus*, *Losillasaurus* and *Mamenchisaurus* (e.g. Young and Zhao, 1972; Dong, 1990; Casanovas, et al, 2001; Ouyang and Ye, 2002; Sekiya, 2011).

The absence of bridged anterior chevrons was considered a synapomorphy of Macronaria (Upchurch, 1995; Wilson and Sereno, 1998; Upchurch et al., 2004; Carballido et al., 2011) or Camarasauromorpha (Salgado et al., 1997, Macronarian clade is recovered herein as a synonymous), suggesting the placement of SHN 181 within Macronaria. Wilson (2002) or D'Emic (2012) recovered this feature as synapomorphy of a more inclusive clade than Macronaria (Wilson, 2002), being present in some rebbachisaurids such as *Limaysaurus* (Carballido et al. 2011) and *Haplocanthosaurus*, a taxon with a uncertain phylogenetic context (Hatcher, 1903; McIntosh and Williams, 1988). This feature is also considered as synapomorphy of Rebbachisauridae (Carballido et al., 2011). Nevertheless, only one anterior chevron SHN 181 was recovered, and it is not possible to exclude the presence of the plesiomorphic condition (bridged chevrons) in more anterior chevrons. Some titanosauriforms might present the plesiomorphic condition such as *Lusotitan* (Lapparent and Zbyszewski, 1957; Mannion et al., 2013; pers. observ., PM), *Dongbeititan* (Wang et al., 2007), *Daxiatitan* (You et al., 2008) and *Xianshanosaurus* (Lü et al., 2009).

The ischia are one of the most diagnostic elements in Valmitão specimen. The presence of a coplanar position for the ischiatic peduncle in SHN 181 suggests its assignation to Macronaria. This condition was considered synapomorphic of Macronaria (Wilson and Sereno, 1998; Wilson, 2002) or Camarasauromorpha (Upchurch et al., 2004) and is present in the Upper Jurassic forms *Camarasaurus* (e.g. Ostrom and McIntosh, 1966), *Giraffatitan* (Janensch, 1961) and *Lourinhasaurus* (Mocho et al., 2014a). Coplanar ischia are also reported outside Macronaria in some rebbachisaurids such as *Limaysaurus*, *Demandasaurus* or *Nigersaurus* (e.g. Upchurch, 1998; Pereda Suberbiola et al., 2003; Torcida Fernández-Baldor et al., 2011; Whitlock, 2011; Carballido and Sander, 2014), *Lapparentosaurus* (pers. observ., PM) or *Haplocanthosaurus* (Hatcher, 1903). Whitlock (2011) and Carballido and Sander (2014) also reported the presence of the apomorphic condition in *Bellusaurus*, *Jobaria* and *Losillasaurus*, but in the last one, the distal end is not totally preserved (Casanovas et al., 2001; pers. observ, PM). The material of *Cetiosaurus leedsi* also present coplanar ischiatic distal ends (Upchurch and Martin, 2003).

12.7.3. Titanosauriform affinities

Other important feature in SHN 181 is the presence of a tuberosity in the lateral face of the ischium without an associated groove that is considered a synapomorphy of Titanosauriformes in the phylogeny proposed by D'Emic (2012). This feature has a wide distribution in Titanosauriformes being present in the basal titanosauriforms *Giraffatitan*, *Venenosaurus* and *Sauroposeidon* (D'Emic, 2012). In the Iberian Peninsula, this condition is present in the Upper Jurassic *Lusotitan* and *Galveosaurus*, and in the Lower Cretaceous *Tastavinsaurus*. *Galveosaurus* have an uncertain phylogenetic position, being considered as a turiasaur (Royo-Torres et al., 2006; 2009, 2012, 2014; Royo-Torres and Upchurch, 2012; Mocho et al., 2014a), a basal macronarian or a basal titanosauriform (Carballido et al., 2011; D'Emic, 2012; Carballido and Sander, 2014). The non-titanosauriforms *Lourinhasaurus* and *Aragosaurus* bear a tuberosity associated with a groove.

SHN 181 presents some features only recognized in more derived titanosauriforms. One of these features is the presence of an ischium smaller than the pubis (ischiatic blade shorter than the pubic blade, following Wilson, 2002). This feature was optimized as a titanosaur synapomorphy (Calvo and Salgado, 1995; Salgado et al., 1997; Upchurch, 1998), but also recovered as

Figure 12.18. Strict consensus of 48 MPTs of 999 steps with a consistency index (CI) of 0.405 and a retention index (RI) of 0.733 obtained from Carballido and Sander (2014) data matrix. Number above and below the nodes indicates the Bremer support and bootstrap values, respectively.

synapomorphy of Nemegtosauridae + (‘*T.*’ *colberti* + Saltasauridae) (Wilson, 2002), *Euhelopus* + ((*Chubutisaurus* + *Wintonotitan*) + Titanosauriformes)) (Carballido et al., 2011) or *Sauroposeidon* + (*Tastavinsaurus* + (Euhelopodidae + (*Chubutisaurus* + Titanosauria))). Furthermore, this feature is also present in several non-titanosaur titanosauriforms such as *Tastavinsaurus* (Canudo et al., 2008), *Qiaowanlong* (You and Li, 2009), *Sauroposeidon* (Rose, 2007), *Tangvayosaurus* (Allain et al., 1999), *Phuwiangosaurus* (Martin et al., 1999), *Huabeisaurus* (D’Emic et al., 2013) and on basal titanosaurs such as *Andesaurus* (Mannion and Calvo, 2011) or *Dreadnoughtus* (Lacovara et al., 2014). In basalmost titanosauriforms and outside Titanosauriformes, the presence of an ischium shorter than the pubis is unreported (e.g. Wilson, 2002; Upchurch et al., 2004; Carballido et al., 2011; D’Emic, 2012; Carballido and Sander, 2014).

A transverse groove on the chevron heads is present in SHN 181 but absent in other Iberian Upper Jurassic sauropods (Yagüe et al., 2006; Mannion et al., 2013; Mateus et al., 2014; Mocho et al., 2014a; Royo-Torres et al., 2014). Similar groove is present in some material referred to *Phuwiangosaurus* (P.W.5-56, Martin et al., 1999; D’Emic, 2012) and was considered as synapomorphy of a clade composed by *Tangvayosaurus*+*Phuwiangosaurus* (D’Emic, 2012). The presence of a transversely compressed iliac peduncle is shared with more derived titanosauriforms, since it could be restricted to Titanosauria (following Mannion and Calvo, 2011). Nevertheless, the transverse compression observed in the iliac peduncle of the pubis of SHN 181 could be due to deformation and will be considered with caution. The femur of SHN 181 has medially beveled tibial and fibular condyles. This feature was considered a synapomorphy of Saltasauridae (Wilson, 2002; D’Emic, 2012), and it is present in SHN 181 probably due deformation.

SHN 181 lacks some features considered as synapomorphies of Titanosauriformes. Haemal channel longer than half of the total chevron length was considered as synapomorphy of Titanosauria by Wilson (2002) or of Titanosauriformes by D’Emic (2012), and absent in SHN 181. This condition is present in several basal titanosauriforms such as *Europasaurus* (Sander et al., 2006; Carballido and Sander, 2014), *Tastavinsaurus* (Canudo et al., 2008; Royo-Torres, 2009), *Giraffatitan* (Janensch, 1950), *Lusotitan* (Lapparent and Zbyszewski, 1957; Mannion et al., 2013); *Cedarosaurus* (Tidwell et al., 1999) and probably *Huanghetitan* (You et al., 2006). Nevertheless, some titanosauriforms present the plesiomorphic condition (short haemal channels) such as *Tambatitanis* (Saegusa and Ikeda, 2014), a referred chevron to *Phuwiangosaurus* (Martin et al., 1999), *Daxiatitan* (You et al., 2008) and in some titanosaurs such as *Wintonotitan* (Hocknull et al., 2009; Poropat et al., 2014), *Uberabatitan* (Salgado and Carvalho, 2008) or *Saltasaurus* (Powell, 1992). The dorsolateral area of SHN 181 femur is not preserved but seems to lack a medial deflection of the proximal one-third with an associated lateral bulge, synapomorphy of Titanosauriformes (Wilson, 2002) or a more inclusive group (Carballido et al., 2011). Some of the synapomorphies supporting Titanosauriformes in the D’Emic (2012) phylogenetic proposal are also absent in SHN 181 such as *i*) anterior caudal vertebrae with bulge or ‘kink’ on ventral margin of caudal ribs; *ii*) a scapula with a ventral process; and *iii*) absence of a corrugated triangular scar on the fibular proximomedial end.

SHN 181 shares several derived conditions with Titanosauriformes such as *i*) caudal ribs posterolaterally projected, surpassing the posterior articulation, *ii*) the presence of a lateral tuberosity of the ischium without an associated groove (both shared with titanosauriforms); *iii*) the presence of an ischium shorted than pubis (common in somphospondylians), *iv*) transverse furrow on the chevron articulations (shared with *Tangvayosaurus* and *Phuwiangosaurus*).

This set of conditions indicates that SHN 181 should be considered as a more derived form than the currently known sauropods of the Portuguese Upper Jurassic, within Titanosauriformes or, inclusively, within Somphospondyli. However this set of characters could also be interpreted as due to a process of convergence with some Cretaceous derived titanosauriforms (e.g.

Phuwiangosaurus, *Tagnvayosaurus*). Therefore it is considered that more material is needed, as well as the reassessment of the established macronarian taxa for the Iberian Upper Jurassic and the study of numerous unpublished specimens of the Upper Jurassic of the Lusitanian Basin (Mocho et al., 2013b, c), in order to improve the phylogenetic approach of SHN 181.

12.7.4. Taxonomic status of SHN 181

Despite the incompleteness of SHN 181, it is possible to recognize an exclusive combination of characters, including local and exclusive autapomorphies. The phylogenetic context of this taxon is not clear, and new discoveries will be important to obtain a more complete vision about this taxon. For the moment, SHN 181 represents a basal Macronaria bearing some local autapomorphies discussed above such as *i*) the transverse furrow on the chevron articulations (shared by *Phuwiangosaurus* + *Tangvayosaurus*); *ii*) ischiatic blade shorted than pubic blade (shared with somphospondylian sauropods); *iii*) fourth trochanter on the midline of the femoral posterior face (shared with *Spinophorosaurus*, *Patagosaurus*, some mamenchisaurids and *Euhelopus*). Beyond these local autapomorphies, SHN 181 also bears some exclusive features that will be commented below.

The neural spines of SHN 181 present some particular features. The presence of lateral depressions in the anterior caudal neural spines is shared with *Aragosaurus ischiaticus*, being considered an autapomorphy of the later taxa by Royo-Torres et al. (2014). Nevertheless, this condition reach a more posterior position on the tail of SHN 181. Furthermore, these lateral depressions are connect dorsally in the most posterior anterior neural spines differing from the condition in *Aragosaurus*. Anteroposterior constricted neural spine apexes are also absent on the holotype of *Aragosaurus* as well as, a longitudinal groove on the dorsal surface. All these features are so far considered as autapomorphies of SHN 181, including the presence of lateral depressions on the neural spines up be clarified the phylogenetic relationship between SHN 181 and *Aragosaurus*, both Iberian Upper Jurassic sauropods. These features on the anterior caudal neural spines were not reported for other Upper Jurassic macronarians (Gilmore, 1925; Janensch, 1950; Ostrom and McIntosh, 1966; McIntosh et al., 1996a, 1996b; Mocho et al., 2014a).

The scapula has several rugosities on the medial and lateral side of the acromial process, unknown in other Upper Jurassic sauropods such as *Lourinhasaurus*, *Dicraeosaurus*, *Giraffatitan* or turiasaurs (Janensch, 1961; Casanovas et al., 2001; Royo-Torres et al., 2006; Mateus et al., 2014; Mocho et al., 2014a). The presence of a ventral concavity bordered medially by a anteroposterior crest in the ventral face of the base of the scapular blade, instead of a ventral process common in titanosauriforms (e.g. Bonaparte et al., 2006; Carballido et al., 2011; Mateus et al., 2011; D'Emic, 2012; Poropat et al., 2014) or in some non-titanosauriforms such as *Lourinhasaurus* (Mocho et al., 2014a) or *Losillasaurus* (Casanovas et al., 2001) is exclusive of this sauropod. A tuberosity in the medial side of the posteriormost part of the acromion process is also considered as an autapomorphy of SHN 181, a similar structure observed in *Saltasaurus* (Powell, 1992).

The distal end of the ischiatic peduncle presents a maximum diameter that corresponds twice its minimum diameter. In sauropods, the maximum diameter is three times or more the minimum one (Wilson, 2002). This feature is considered as autapomorphic of SHN 181.

In lateral view, the fibula present a pronounced sigmoidal profile with a marked defection of the proximal end, a shared feature with *Camarasaurus* and *Haplocanthosaurus* (Ikejiri, 2004). The fibular proximal end SHN 181 presents a well-defined rectangular outline bearing a shoulder below the anterior trochanter, also present in some specimens of *Camarasaurus supremus* (YPM 1910, USNM 13786, Ikejiri, 2004). Nevertheless, a well-defined rectangular morphology of the fibular proximal end in lateral/medial view is retained tentatively as an autapomorphy of SHN 181.

In conclusion, SHN 181 is featured by the following exclusive combination of characters: (1) sagittal longitudinal groove in the most proximal caudal neural spines; (2) apex of the most anterior caudal neural spines anteroposterioly constricted, resulting in an X in dorsal view; (3) anterior caudal vertebrae with a medial accessory articulation on the prezygapophyses, (4) lateral depression on the apex of the caudal neural spines (shared with *Aragosaurus*); (5) transverse furrow on the chevron articulations (shared by *Phuwiangosaurus* + *Tangvayosaurus*); (6) circular rough tuberosity in the medial side of the scapula; (7) elliptical concavity on the ventral face of the scapular blade base; (8) the maximum diameter of the ischiatic distal end being twice the minimum one; (9) ischium shorter than pubis (shared with titanosaurs); (10) robust fourth trochanter located in midline of the femoral diaphysis posterior face, (shared with *Euhelopus*, *Mamenchisaurus* and *Omeisaurus*); and (11) rectangular morphology of fibular proximal end in lateral/medial view.

12.7.5. SHN 181 in the contest of Iberian sauropods

SHN 181 corresponds to a undescribed form for the Iberian Upper Jurassic and might be distinguished from the previously established sauropod taxa, *Lourinhasaurus alenquerensis* (Lapparent and Zbyszewski, 1957; Dantas et al., 1998; Mocho et al., 2014a), *Lusotitan atalaiensis* (Lapparent and Zbyszewski, 1957; Antunes and Mateus, 2003; Mannion et al., 2013), *Dinheirosaurus lourinhanensis* (Bonaparte and Mateus, 1999; Mannion et al., 2012), *Zby atlanticus* (Mateus, 2005; Mateus et al., 2014), *Aragosaurus ischiaticus* (Sanz et al., 1987; Royo-Torres et al., 2014), *Turiasaurus riodevensis* (Royo-Torres et al., 2006; Royo-Torres and Upchurch, 2012), *Losillasaurus giganteus* (Casanovas et al., 2001; Gascó, 2009), and *Galveosaurus herreroi* (Sánchez-Hérnandez, 2005; Barco, 2009). Besides the set of autapomorphies proposed, there are some characters that allow discriminating SHN 181 of the rest of Upper Jurassic Iberian sauropods.

Lourinhasaurus and *Aragosaurus* bear several differences that distinguished them from SHN 181: *i*) ischium with a tuberosity on lateroventral associated to a groove; *ii*) ischium and pubis with similar size; and *iii*) fourth trocanther located on medioposterior border of the diaphysis. *Lourinhasaurus* also presents a circular sprf on the anterior caudal vertebrae (autapomorphy of *Lourinhasaurus alenquerensis*, Mocho et al., 20014a), fan-to-delta-like morphology of the neural spines (shared with *Camarasaurus grandis* and *C. supremus*; Ikejiri, 2004; Ikejiri et al., 2005) and a ventral process on ventral margin of base of the scapular blade, not present in SHN 181. Despite the differences observed in both taxa, *Aragosaurus* shares with SHN 181 the presence of lateral depressions on the caudal neural spine apex, previously considered as an exclusive autapomorphy of *Aragosaurus* (Royo-Torres et al., 2014). The lateral bulge present on the lateral side of the *Aragosaurus* femur is considered absent in the Valmitão specimen.

Lusotitan could be distinguished from SHN 181, by the presence of: *i*) dorsoventrally compressed anterior and middle caudal centra; *ii*) bridged chevrons (although the bridged condition can not totally excluded in SHN 181), *iii*) absence of a transverse furrow on the chevron articulations, *iv*) deep haemal channel, *v*) a curved tibia (autapomorphy of *Lusotitan*), *vi*) second cnemial crest on the tibia, and *vii*) short and soft tibial scar in the fibula. No autapomorphies proposed by Mannion et al. (2013), possible to evaluate, are present in SHN 181.

As we referred above, several features suggested the exclusion of SHN 181 from the Dipodocoidea lineage. *Dinheirosaurus* exhibits several differences on the caudal vertebrae when compared with SHN 181. *Dinheirosaurus* anterior caudal vertebrae are procoelous, with ventral hollow border by pronounced ventrolateral crests, pleurocoels and concave zygapophyses (pers. observ., PM), features absent on SHN 181 and in *Lourinhasaurus*, *Lusotitan*, *Aragosaurus* and *Losillasaurus*.

In *Losillasaurus*, the presence of procoelous caudal vertebrae, expanded anterior caudal zygapophyses, tubercle on the ventral margin of base of scapular blade, not pronounced acromial ridge, flat area behind the acromial ridge and ischium with no lateral tuberosity and with a lateroventral groove allow to distinguish it from SHN 181. The description of all *Turiasaurus riodevensis* material is in progress, but there are features referred on Royo-Torres et al. (2006) or provided by in situ observation, that allow us to differentiate it from Valmitão sauropod. As in *Losillasaurus*, the presence of a ventral tuberosity on the scapula, not pronounced acromial ridge, and flat area behind the acromial ridge featured *Turiasaurus* and are not present in SHN 181. The *Turiasaurus* fibula is also different from the fibula of SHN 181, presenting a concave and wide lateral trochanter and a short tibial scar (pers. observ., PM).

Zby atlanticus presents some differences with SHN 181, such as the absence of an excavated area behind the acromial ridge that is present in neosauropods (Upchurch et al., 2004). *Zby* presents bridged chevrons and does not share with SHN 181 the presence of transverse furrow on the chevron articulations. *Galveosaurus* is particularly difficult to differentiate from SHN 181 or *Lusotitan*. When comparing with Valmitão sauropod, *Galveosaurus* might be distinguished by the presence of a flat scapular blade cross-section (against the D-shaped outline in SHN 181). For the moment, no significant differences were found between *Lusotitan* and *Galveosaurus*. The redescription of *Galveosaurus* is needed in order to test the validity of this taxon as well as, its phylogenetic context.

12.8. CONCLUSIONS

The detailed description of a partial skeleton of a sauropod found in Valmitão (Lourinhã) in sediments of the Praia de Amoreira-Porto Novo Formation (upper Kimmeridgian-basal Tithonian) allows to diagnose a new genus and species. SHN 181 is featured by the presence of sagittal longitudinal groove in the most proximal caudal neural spines; apex of the most anterior neural spines anteroposterioly constricted, resulting in an X in dorsal view; anterior caudal vertebrae with a medial accessory articulation on the prezygapophyses; lateral depression on the apex of the neural spines; transverse furrow on the chevron articulations; circular rough tuberosity in the medial side of the posteriormost part of the acromion process; elliptical concavity on the ventral face of the scapular blade base; the maximum diameter of the ischiatic distal end is twice the minimum one; ischium shorted than pubis; robust fourth trochanter located in midline of the femoral posterior face; and rectangular morphology of fibular proximal end in lateral/medial view. Some of these features are previously unreported for Upper Jurassic sauropods and just shared by some Cretaceous titanosauriforms.

Despite the incompleteness of the specimen, the placement of SHN 181 within Camarasauromorpha is supported by the presence of procoelous/distoplatyan caudal centra and the fibular facet for the astragalus facing laterally. In the proposed phylogenetical analysis the taxon is recovered at the base of Camarasauromorpha in a polytomy including *Europasaurus*, *Galveosaurus*, *Bellusaurus*, *Euhelopus*, *Tastavinsaurus*, *Tehuelchesaurus*, *Camarasaurus*, SHN 181, *Chubutisaurus*, *Brachiosaurus*, *Giraffatitan*, *Paluxysaurus*, *Venenosaurus*, *Cedarosaurus*, *Erketu* and ((*Wintonotitan* + *Tendaguria*) + and more derived titanosauriforms)). SHN 181 shares several features with Titanosauriformes: *i*) caudal ribs posterolaterally projected surpassing the posterior articulation; *ii*) the presence of a lateral tuberosity of the ischium without an associated groove; *iii*) the presence of an ischium shorter than the pubis (common in somphospondylians), and *iv*) transverse furrow on the chevron articulations (shared by *Tangvayosaurus* and *Phuwiangosaurus*).

The presence in SHN 181 of several derived conditions is particularly interesting. This could indicate a process of convergence with Cretaceous derived titanosauriforms or that SHN

181 has to be placed within Titanosauriformes, or, inclusively, within Somphospondyli, in a more derived position than any currently known sauropod in the Portuguese Upper Jurassic. In any case, more material is needed in order to improve the present phylogenetic approach.

The paleobiodiversity of the Lusitanian Basin Upper Jurassic sauropod faunas is updated being composed by turiasaur *Zby atlanticus*, the diplodocid *Dinheirosaurus lourinhanensis*, and three basal macronarians: the camarasaurid *Lourinhasaurus alenquerensis*, the basal macronarian *Lusotitan atalaiensis* (a possible brachiosaurid) and the camarasauromorph SHN 181.

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12.10. REFERENCES

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CHAPTER 13

Phylogenetic context of the Upper Jurassic Sauropods of the Lusitanian Basin (Portugal)

Phylogenetic context of the Upper Jurassic Sauropods of the Lusitanian Basin (Portugal)

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13.1. INTRODUCTION

Sauropods are one of the best-represented vertebrate groups in the Mesozoic fossil record of the Lusitanian Basin, particularly in the Upper Jurassic. The first occurrences were documented by Sauvage (1897-98), and the first well-supported taxa were not published until the middle of the 20th century, such as the species *Apatosaurus alenquerensis* and *Brachiosaurus atalaiensis* (Lapparent and Zbyszewski, 1957), now considered as distinct genus, *Lourinhasaurus alenquerensis* and *Lusotitan atalaiensis*.

In the late 20th century, this record starts to be reviewed and new discoveries were published. One of the most important discoveries was the type specimen of *Dinheirosaurus lourinhanensis* in the Upper Jurassic of the Praia de Amoreira-Porto Novo Formation (Dantas et al., 1992; Bonaparte and Mateus, 1999), considered as a diplodocid more closely related to Diplodocinae than to Apatosaurinae (Rauhut et al., 2005; Whitlock, 2011; Mannion et al., 2012; Tschopp and Mateus, 2013; Tschopp et al., 2015).

Previous to the first phylogenetic approaches based on cladistics analyses, it was hypothesized that the Portuguese Upper Jurassic sauropod fauna was mainly composed by diplodocids, brachiosaurids and basal macronarians, probably camarasaurids (Lapparent and Zbyszewski, 1957; McIntosh, 1990a, b; Bonaparte and Mateus, 1999; Antunes and Mateus, 2003). Upchurch et al. (2004) proposed one of the first cladistic analysis considering a Portuguese Upper Jurassic sauropod. In this analysis, *Lourinhasaurus* scoring was based on the lectotype specimen and a second specimen that at that time was already considered as the holotype of *Dinheirosaurus lourinhanensis*. The result of this analysis considered *Lourinhasaurus* as a basal eusauropod. *Lourinhasaurus* was incorporated in several other cladistic analyses being considered as a basal macronarian (Royo-Torres et al., 2006; Barco, 2010), or as a neosauropod non-macronarian (Royo-Torres and Upchurch, 2012; Royo-Torres et al., 2012). More recently, with the revision of *Lourinhasaurus* lectotype, this taxon was related with the Camarasauridae clade (Mocho et al., 2014a), posteriorly supported by Royo-Torres et al. (2014a) and Tschopp et al. (2015). *Lourinhasaurus* was considered as a close related form to *Camarasaurus* (McIntosh, 1990a, b; Wilson and Sereno, 1998; Mocho et al., 2014a).

Dinheirosaurus was the second Portuguese taxa to be included in phylogenetic analyses. In the Rauhut et al. (2005) phylogenetic hypothesis, *Dinheirosaurus* is recovered as a diplodocine, in polytomy with *Tornieria*, *Diplodocus* and *Barosaurus*. Whitlock (2011) cladistic analysis also obtained *Dinheirosaurus* as a diplodocine more primitive than Morrison Formation diplodocines, *Barosaurus* and *Diplodocus*. Mannion et al. (2012) provided a detailed description of the *Dinheirosaurus* holotype (not including the unprepared material), and considered *Dinheirosaurus* as a basal diplodocine and sister taxa of *Supersaurus*, both forming a monophyletic clade. This hypothesis was supported by the phylogeny proposed by Tschopp and Mateus (2013). Mocho et al. (2014a) propose a more derived position for *Dinheirosaurus lourinhanensis*, nevertheless, recent diplodocid specimen-level analyses support Mannion et al. (2012) and Tschopp et al. (2015) phylogenetic hypotheses. Furthermore, Tschopp et al. (2015) proposed the allocation of the Portuguese taxon within *Supersaurus* genus, proposing a new combination, *Supersaurus lourinhanesis*.

Lusotitan atalaiensis was redescribed and incorporated in a phylogenetic context by Mannion et al. (2013a) considering it as a basal macronarian, and brachiosaurid with doubt. Previously, Torcida Fendández-Baldor (2012) also obtained a similar position for *Lusotitan* as a basal macronarian more primitive than *Camarasaurus*.

An incomplete specimen found in Praia da Areia Branca (Bombarral Formation, Tithonian), and composed by a partial tail, was also incorporated in a phylogenetic analysis based on the Upchurch et al. (2004) data matrix. This analysis suggested that Praia de Areia Branca sauropod corresponds to a basal macronarian.

Several other sauropod specimens recovered in the Upper Jurassic sediments of the Lusitanian Basin were not yet incorporated in any phylogenetic analyses. *Zby atlanticus* was established by Mateus et al. (2014). The type specimen of *Zby atlanticus* was firstly considered as *Camarasaurus* sp. (Mateus, 2005) and *Turiasaurus riodevensis* (Mateus, 2009). Mateus et al. (2014) related this taxon to the Turiasauria clade, hypothesis earlier suggested by several authors (Mateus, 2009; Royo-Torres et al., 2009, 2014b; Mocho et al., 2012; Royo-Torres and Upchurch, 2012).

Recent studies suggest that Iberian sauropods are represented by endemic genera (Dantas et al., 1998; Bonaparte and Mateus, 1999; Casanovas et al., 2001; Antunes and Mateus, 2003; Sánchez-Hernández, 2005; Royo-Torres et al., 2006; Mateus et al., 2014) closely related to groups well represented in other continents during the Upper Jurassic such as brachiosaurids (Antunes and Mateus, 2003; Mannion et al., 2013a), diplodocids (Bonaparte and Mateus, 1999; Mannion et al., 2012; Mocho et al., 2014b) or camarasaurids (Mocho et al., 2014a). The supposed close relationship of the Portuguese sauropods with taxa from the North American Upper Jurassic Morrison Formation (e.g. Lapparent and Zbyszewski, 1957) is less patent than in other dinosaur groups (e.g. Galton, 1980; Pérez-Moreno et al., 1999; Mateus and Antunes, 2003; Malafaia et al., 2007, 2010, 2015; Hendrickx and Mateus, 2014).

This study proposes the first phylogenetic analysis including all sauropod species for the Portuguese Upper Jurassic (i.e. *Lourinhasaurus alenquerensis*, *Dinheirosaurus lourinhanensis*, *Lusotitan atalaiensis* and *Zby atlanticus*); and also incorporates all Spanish Upper Jurassic species (*Turiasaurus riodevensis*, *Galveosaurus herreroi*, *Aragosaurus ischiaticus* and *Losillasaurus giganteus*), as well as several sauropod forms from the Morrison and Tendaguru Formations (*Diplodocus*, *Apatosaurus*, *Barosaurus*, *Kaatedocus*, *Haplocanthosaurus*, *Brachiosaurus*, *Camarasaurus*, *Supersaurus*, *Tornieria*, *Giraffatitan* and *Dicraeosaurus*). This integrative analysis tries to provide a new phylogenetic approach for the Upper Jurassic sauropod fauna from the Lusitanian Basin and to improve our knowledge about phylogenetic relationships of other contemporaneous sauropods.

13.2. ANATOMICAL ABBREVIATIONS

acp, acromial process; cpol, centropostzygapophyseal lamina; dpc, deltopectoral crest; dv, dorsal view; gl, glenoid; lat.cpol, lateral centropostzygapophyseal lamina; lv, lateral view; Mc, metacarpal; mv, medial view; pacdf, parapophyseal centrodiapophyseal fossa; pcdl, posterior centrodiapophyseal lamina; pcpl, posterior centroparapophyseal lamina; podl, postzygadiapophyseal lamina; posl, postspinal lamina; prdl, prezygadiapophyseal lamina; prsl, prespinal lamina; spol, spinopostzygadiapophyseal lamina; sprl, spinoprezygadiapophyseal lamina; vv, ventral view.

13.3. INSTITUTIONAL ABBREVIATIONS

MG, Museu Geológico do Laboratório Nacional de Energia e Geologia, Lisboa, Portugal; ML, Museu da Lourinhã, Lourinhã, Portugal; SHN, Sociedade de História Natural, Torres Vedras, Portugal (plus (JJS) for the José Joaquim dos Santos collection deposited in the Sociedade de História Natural).

13.4. MATERIAL

The present phylogenetic analysis is based on a dataset composed by 464 morphological characters, mainly based on those proposed by Salgado et al. (1997), Wilson and Sereno (1998), Wilson (2002), Upchurch et al. (2004), Curry Rogers (2005), González Riga et al. (2009), Whitlock (2011), Santucci and Arruda-Campos (2011), Zaher et al. (2011), D'Emic (2012), Carballido et al.

(2012), Mannion et al. (2012, 2013) and Tschopp et al. (2015). Some characters were modified based on personal observations and some new characters are proposed.

The present dataset is composed by 95 taxa and three unpublished specimens (see S.21, S.22) that are two partial skeletons from the Praia de Amoreira-Porto Novo Formation (upper Kimmeridgian-basal Tithonian) of Valmitão (Lourinhã, Portugal) and one of the specimens (EC1) recovered in the "Lo Hueco" site (e.g. Díez-Díaz et al., 2014; Ortega et al., 2015) where outcrops the upper Campanian-lower Maastrichtian sediments of the "*Margas, Arcillas y Yesos de Villalba de la Sierra*" Fm. In this data matrix, it also included the unpublished scoring for *Spinophorosaurus nigerensis* based on the holotype and paratype material, and under description by the present author. The operational taxonomic units were scored based on personal observations, published descriptions, photographs from fellow researchers and previous published scorings (see S.21).

The present analyses try to obtain an integrative phylogenetic analysis for the Upper Jurassic sauropods of the Lusitanian Basin. All Portuguese taxa were scored based on personal observations including the lectotype material of *Lourinhasaurus alenquerensis* (Lapparent and Zbyszewski, 1957; Dantas et al., 1998; Antunes and Mateus, 2003; Mocho et al., 2014a) and *Lusotitan atalaiensis* (Lapparent and Zbyszewski, 1957; Antunes and Mateus, 2003; Mannion et al., 2013a) housed in the Museu Geológico (Lisboa, Portugal); *Dinheirosaurus lourinhanensis* (Dantas et al., 1992; Bonaparte and Mateus, 1999; Mannion et al., 2012) and *Zby atlanticus* (Mateus, 2005; Mateus et al., 2014) holotypes housed in the Museu da Lourinhã (Lourinhã, Portugal). As was referred above, two other specimens housed in the Sociedade de História Natural (Torres Vedras, Portugal) and collected in the Upper Jurassic sediments of Valmitão (SHN (JJS) 177 and SHN 181) was including in the analyses. One of them, the specimen SHN 181, might represent a new taxon.

In particular, the direct observation on *Dinheirosaurus* holotype and unpublished field information allows us to provide a new scoring for this taxon found in the cliffs of Porto Dinheiro (Praia de Amoreira-Porto Novo Formation; Dantas et al., 1992, 1998). Nevertheless, this specimen is not fully prepared and some aspects concerning to the neural spine morphology of cervical and dorsal vertebrae are difficult to access (see Systematic Paleontology).

The present dataset also incorporates all Spanish sauropod species established for the Villar del Arzobispo Formation (Tithonian-Berriasian). The paleogeographic areas occupied by Portuguese and Spanish sauropods are geographically close, if not the same, during the Upper Jurassic. The phylogenetic relationships between these faunas are important in order to understand the evolutionary history of this group and the paleobiogeographic role of the Iberian Peninsula. This dataset also includes several sauropod taxa of Morrison Fm. and Tendaguru Fm., being excluded *Austrolodocus bohetii*, *Tendaguria tanzaniensis* and *Janenschia robusta* due the incompleteness of the type specimens (Bonaparte et al., 2000; Remes 2006).

13.5. PHYLOGENETIC ANALYSIS

A dataset composed by 464 characters and 95 taxonomic units were analyzed using TNT 1.1 (Goloboff et al, 2003) in order to obtain the most parsimonious trees (MPTs). All multi-state characters were treated as unordered (#2, #3, #12, #61, #62, #88, #98, #99, #100, #101, #107, #108, #111, #113, #115, #121, #124, #133, #144, #164, #170, #171, #175, #177, #179, #180, #181, #183, #189, #194, #195, #196, #206, #209, #217, #224, #231, #233, #234, #240, #254, #272, #274, #276, #278, #279, #302, #303, #323, #335, #356, #398, #408). We used a heuristic tree search performing 1000 replications of Wagner trees (using random addition sequences) followed by tree bisection reconnection (TBR) as swapping algorithm, saving 100 trees per replicate. To test the support of the phylogenetic hypotheses, Bremer support and bootstrap (absolute frequencies based on 10000 replicates) values were obtained in TNT 1.1.

The analysis yielded 384 MPTs of 1508 steps with a consistency index (CI) of 0.351 and a retention index (RI) of 0.755 (Figs. 13.1, 13.2). The general topology recovers the major nodes obtained by previous phylogenetic approaches (e.g. Wilson, 2002; Upchurch et al., 2004; D'Emic, 2012; Carballido and Sander, 2014), including Eusauropoda, Neosauropoda, Diplodocoidea, Macronaria, Camarasauromorpha, Brachiosauridae, Somphospondyli, Euhelopodidae, Titanosauria, Aeolosaurini and Saltasauridae, and also, Camarasauridae, recently proposed as a monophyletic clade (Mocho et al., 2014a).

The strict consensus tree shows several important polytomies:

i) At the base of Rebbachisauridae, composed by *Zapalasaurus*, *Histriasaurus*, *Comahuesaurus*, (*Rayosaurus* + *Rebbachiasaurus* + (*Limaysaurus* + *Cathartesaura*) and (*Nigersaurus* + *Demandasaurus*) (Fig. 13.1).
ii) At the base of Diplodocinae, composed by *Tornieria*, *Supersaurus*, *Kaatedocus* and *Dinheirosaurus* + (*Barosaurus* + (*Diplodocus* + SHN (JJS) 177)) (Fig. 13.1).
iii) At the base of Titanosauriformes, composed by *Galveosaurus*, Brachiosauridae and more derived titanosauriforms than brachiosaurids (Fig. 13.2).
iv) At the base of Brachiosauridae, composed by *Lusotitan*, *Brachiosaurus*, *Giraffatitan*, *Abydosaurus* and laurasiforms sauropods (*Cedarosaurus*, *Tastavinsaurus*, *Sonorasaurus* and *Venenosaurus*) (Fig. 13.2).
v) Within euhelopodids, including *Huabeisaurus*, *Yunmenglong*, *Erketu* and (*Euhelopus* + *Daxiatitan*) (Fig. 13.2).
vi) Within Titanosauria, including *Aeolosaurus rionegrinus*, *A. colhuehuapensis* and *Gondwanatitan* (Fig. 13.2).
vii) Within Saltasaurinae, formed by *Trigonosaurus*, *Saltasaurus* and *Neuquensaurus* (Fig. 13.2).

Concerning with the Portuguese Upper Jurassic sauropods, *Zby atlanticus* is recovered as a non-neosauropod eusauropod within Turiasauria (Fig. 13.1), as sister taxa of *Turiasaurus riodevensis* from the Tithonian-Berriasian of Spain (Royo-Torres et al., 2006). The phylogenetic position of *Zby atlanticus* within Turiasauria is supported by the presence of dorsoventrally constricted humeral deltopectoral crest (#326), humeral distal condyles exposed on the distal end of the anterior face (#329), strong bulge at the level of the deltopectoral crest on the humeral posterior face (#333) and deeply concave posterior face of the humeral distal end (#337). *Zby atlanticus* and *Turiasaurus riodevensis* resulted in a monophyletic group supported by only one synapomorphy: distal end of the radius beveled 20º (#347).

The present analysis recovered *Dinheirosaurus* within Diplodocinae, in a position more derived than *Kaatedocus*, *Supersaurus* and *Tornieria* (Fig. 13.1). The inclusion of *Dinheirosaurus* within Diplodocoidea is supported by the presence of middle and posterior dorsal neural spines lacking triangular aliform process (#196); neural arch much taller than pedicel in middle and posterior dorsal vertebrae (#216); well-developed prespinal laminae (prsl) in anterior caudal vertebrae and visible in lateral view (#254); spinoprezygapophyseal laminae (sprl) extending onto lateral aspect of the neural spine (#261); dorsally developed and medially restricted postspinal lamina (posl) (#264). The placement of *Dinheirosaurus* into Flagellicaudata is supported by a divided centropostzygapophyseal lamina (cpol) on middle and posterior dorsal vertebrae (#190) and slight procoelous anterior caudal vertebrae (#240). *Dinheirosaurus* is placed into Diplodocidae by the presence of a subvertical lamina between the ventral surface of the postzygadiapophyseal lamina (podl) and the pcdl on the posterior cervical vertebrae (#155); accessory lamina linking the hyposphene up to the base of the pcdl on middle and posterior dorsal vertebrae (#184); and "wing-like" anterior caudal ribs (#251). Furthermore, the position of *Dinheirosaurus* within Diplododocinae is supported by: posterior projected tpol from cpol on cervical vertebrae (#134); zygapophyses transversely convex on posterior cervical vertebrae (#146); dorsoventrally elongated coel posteriorly to the sprl on the posterior cervical vertebrae (#154); pleurocoels on anterior caudal centra (#243);

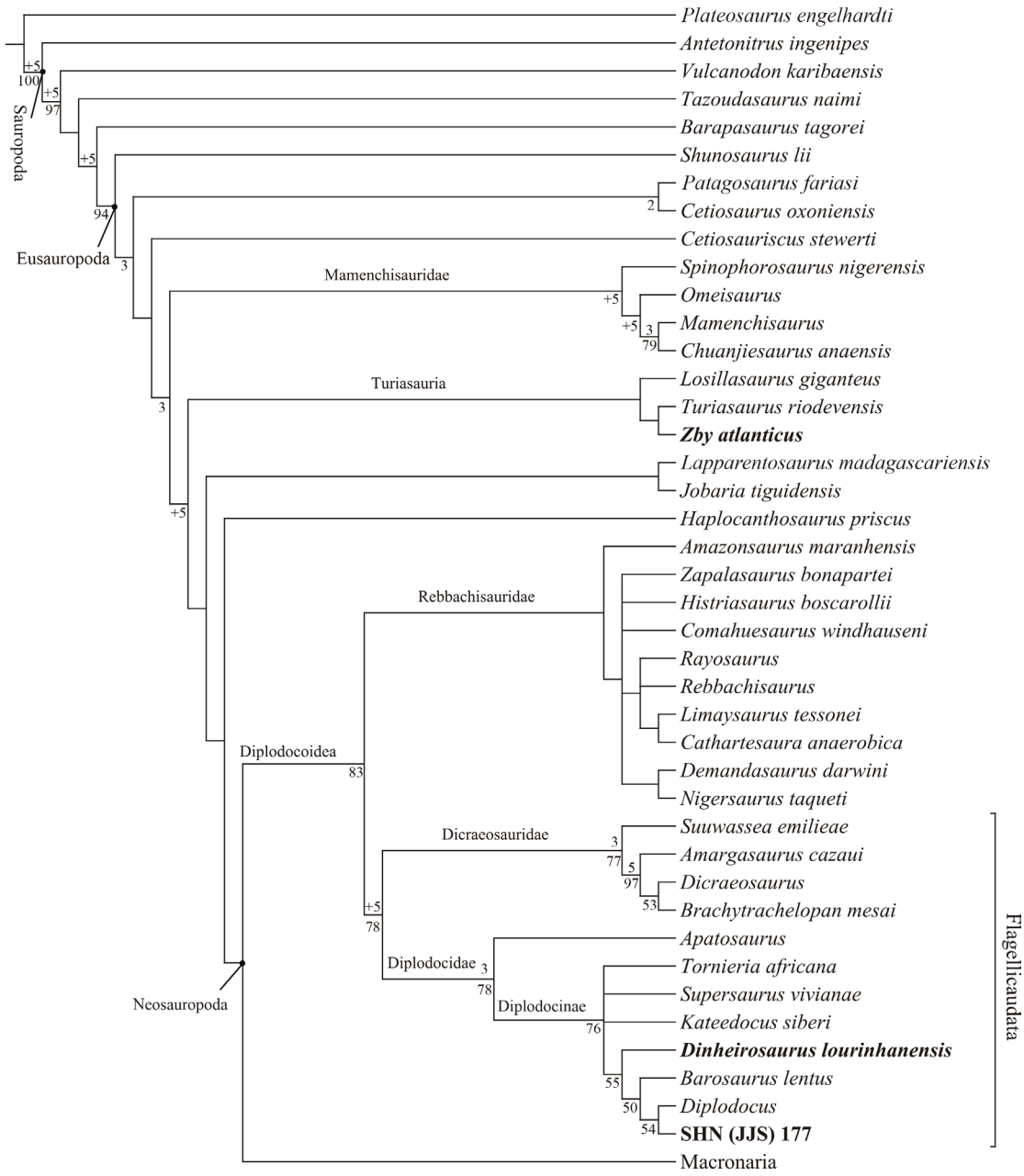

Figure 13.1. Strict consensus of 384 MPTs of 1508 steps with a consistency index (CI) of 0.351 and a retention index (RI) of 0.755 for the present data matrix. The present cladogram only includes the non-macronarians (for Macronaria see the figure 2). Number in the nodes indicates the bootstrap values (below, only de values higher than 50) and the Bremer support values (above, only the values higher than 1).

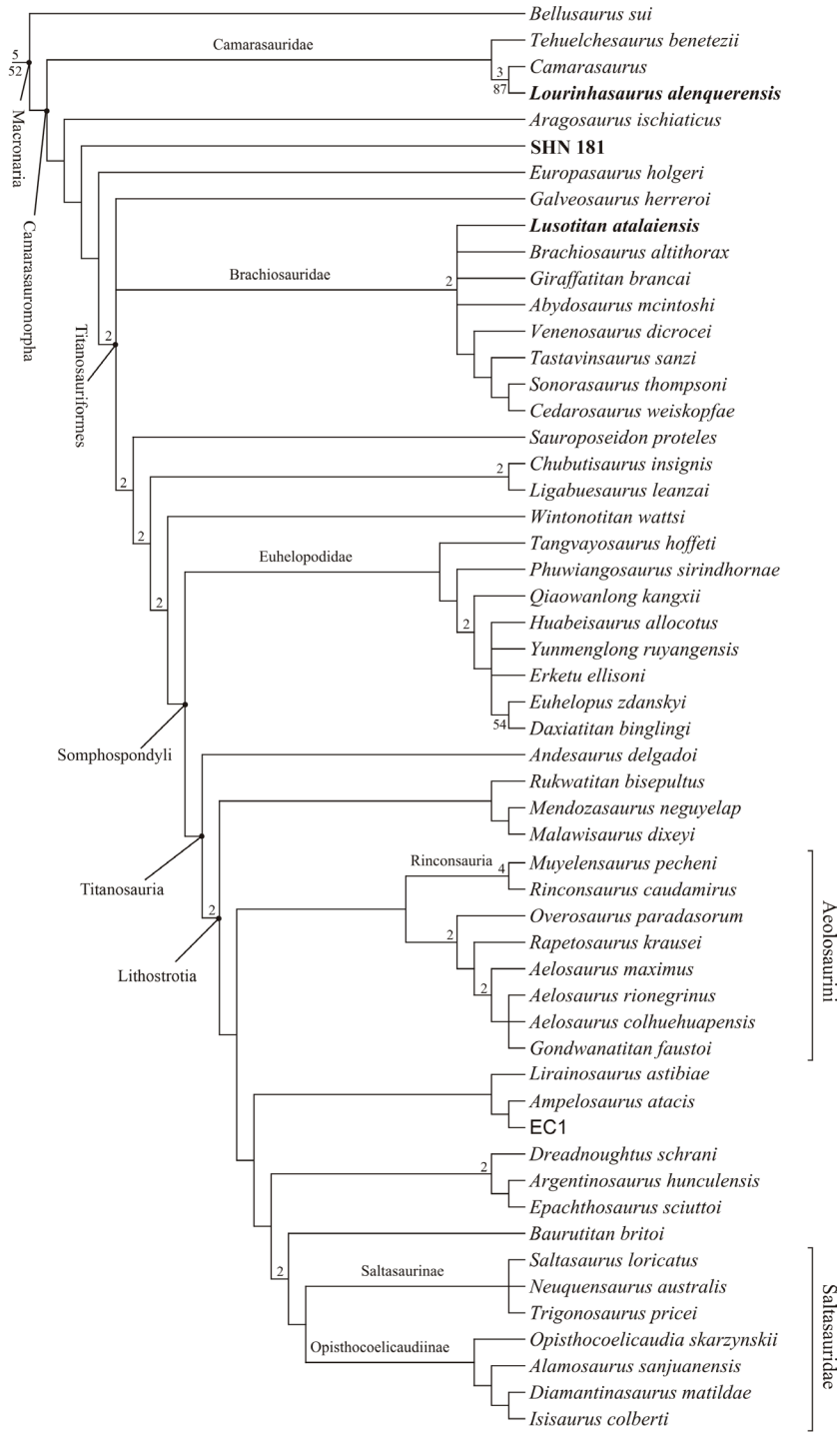

Figure 13.2. Strict consensus of 384 MPTs of 1508 steps with a consistency index (CI) of 0.351 and a retention index (RI) of 0.755 for the present data matrix. The present cladogram only includes the macronarian sauropods (for non-macronarians see the figure 1). Number in the nodes indicates the bootstrap values (below, only de values higher than 50) and the Bremer support values (above, only the values higher than 1).

the ventral face is transversely concave on proximal anterior caudal vertebrae (#245); anterior and middle caudal vertebrae with well-developed ventrolateral ridges (#246); anterior and middle caudal vertebrae with a ventral hollow (#247) and dorsally bifurcated anterior caudal neural spine (#266). *Dinheirosaurus* is in a more derived position than *Supersaurus*, *Kaatedocus* and *Tornieria*, into a clade with *Barosaurus* and *Diplodocus* + SHN (JJS) 177 and supported by the presence of a coel posteroventrally located to the pleurocoel (#126, present in *Tornieria* and absent in *Kaatedocus*, *Supersaurus*); rough lateral aspect of the prezygadiapophyseal lamina (prdl) on posterior cervical vertebrae (#153, absent in *Kaatedocus* and *Supersaurus*, and unknown in *Tornieria*); an vertical accessory lamina posteriorly to the sprl (#156, absent in *Kaatedocus* and *Supersaurus*, and unknown in *Tornieria*); well-developed dorsal bifurcation on anterior caudal neural spines (#267, absent in *Tornieria* and *Supersaurus*, and unknown in *Kaatedocus*); and anterior caudal vertebrae with concavo-convex zygapophyseal articulations (#269, absent in *Tornieria* and *Supersaurus*, and unknown in *Kaatedocus*). No potencial autapomorphies based in the used data matrix were recovered for *Dinheirosaurus lourinhanensis* (see diagnosis on Systematic Paleontology).

SHN (JJS) 177 is a specimen from Valmitão (Lourinhã) previously related to Diplodocidae, concretely, to Diplodocinae (Mocho et al., 2014b), position supported by the present analysis (Fig. 13.1). The relationships of this sauropod with the Diplodocidea is supported by the presence of well-developed prsl in anterior caudal vertebrae and visible in lateral view (#254), sprl extending onto lateral aspect of the neural spine (#261); and dorsally developed and medially restricted posl (#264). The placement of the Valmitão specimen within Flagellicaudata is sustained by slight procoelous anterior caudal vertebrae (#240); dorsal bridged anterior chevrons (#292); V-shaped cross-sectional shaped of the ischiatic distal ends (#387); distal end strongly and dorsoventrally expanded (#388); triangular shape of the ischiatic distal end (#396). The SHN (JJS) 177 is included in Diplodocidae by the existence of "wing-like" anterior caudal ribs (#251); diapophyseal laminae on the anterior caudal ribs (#257); and the sprl-spinopostzygapophyseal lamina (spol) contact (#262). SHN (JJS) 177 occupies a derived position within Diplodocinae supported by the presence of pleurocoels in the anterior caudal vertebrae (#243); transversely concave ventral face on the proximal anterior caudal vertebrae (#245); well-developed ventrolateral ridges on anterior and middle caudal vertebrae (#246); a ventral hollow on anterior and middle caudal vertebrae (#247); and dorsally bifurcated anterior caudal neural spines (#266). In the present analysis, SHN (JJS) 177 is the sister taxon of *Diplodocus*. This sauropod shares with *Dinheirosaurus*, *Barosaurus* and *Diplodocus* a well-developed dorsal bifurcation on anterior caudal neural spines (#267) and anterior caudal vertebrae with concavo-convex zygapophysal articulations (#269). SHN (JJS) 177 shares with *Diplodocus* the presence of pre-epipophyses on the anterior caudal vertebrae, a potential synapomorphy of the clade SHN (JJS) 177 + *Diplodocus*.

Concerning to *Lourinhasaurus alenquerensis*, the present phylogenetic approach supports the phylogenetic position recently proposed by Mocho et al. (2014a) as a member of Camarasauridae, a monophyletic clade, which includes *Camarasaurus* and *Tehuelchesaurus* (for a detailed discussion see Mocho et al., 2014a) (Fig. 13.2). *Lourinhasaurus* is considered herein as a macronarian camarasauromorph. The placement of *Lourinhasaurus* within Macronaria is supported by the following synapomorphies: *i*) height/width ratio for the posterior articulation of the cervical centra is 0,9-07 (#121); *ii*) middle and posterior dorsal centra slightly compressed dorsoventrally (height/width ratio is 1-0.8, #195); *iii*) opisthocoelous posterior dorsal vertebrae (#209); *iv*) acromial process lies nearly the midpoint of scapular body (#306); and *v*) flat and almost coplanar distal ischiatic end (#387). The present analysis only recovers a synapomorphy for Camarasauromorpha (cervical ribs are elongate and form overlapping bundles, #162), but it is not possible to confirm its presence on the *Lourinhasaurus* lectotype. *Lourinhasaurus*, *Camarasaurus* and *Tehuelchesaurus* were recovered in a monophyletic group, corresponding to the Camarasauridae clade. Camarasauridade clade is supported by two synapomorphies: the absence of a prsl on the dorsal vertebrae (#174) and the presence of

a wide medial fossa on dorsal neural spines (#177), both not possible to test in the preserved material of *Lourinhasaurus*. Finally, *Camarasaurus* and *Lourinhasaurus* correspond to a monophyletic clade, supported by three synapomorphies: anterior and middle non-bifid dorsal neural spines with a transversely concave dorsal margin (#215); scapular blade with a rounded expansion on the acromial side (#152); and the angle between the ischiatic peduncle and the acetabulum is less than 60º (#397).

SHN 181 is a sauropod specimen collected from Vamitão cliffs (Lourinhã) close to the SHN (JJS) 177 fossil site. This specimen bears several important differences with the other Upper Jurassic taxa of the peri-North Atlantic area, and probably represents a new sauropod taxon (see Chapter 12). In the proposed phylogenetic approach, this specimen is recovered as a stem titanosauriform macronarian (Fig. 13.2). The placement within Macronaria is supported by the presence of a flat and almost coplanar distal ischiatic end (#387). As in the case of *Lourinhasaurus*, in SHN 181 is not possible to test the presence of the unique synapomorphy that sustain the Camarasauromorpha clade in this phylogenetic hypothesis. *Aragosaurus* + (SHN (181 + (Titanosauriformes)) his supported by three synapomorphies, two of them present in SHN 181: the absence of hyposphene ridge on anterior caudal vertebrae (#256) and the presence of chevrons with composed articular surfaces (#296). In this phylogenetic approach, SHN 181 is more derived than *Aragosaurus* and more primitive than *Europasaurus*, which represent the sister taxa of the Titanosauriformes. The clade SHN 181 + (*Europasaurus* + Titanosauriformes) is supported by two synapomorphies: pubis larger (around 120% or more) than the ischium (#379) and an ischium tuberosity without an associated groove (#390). SHN 181 does not share with the Titanosauriformes clade (supported herein by eight synapomorphies) the presence of dorsoventrally compressed anterior caudal vertebrae (excluding the most proximal vertebrae, #287). Is important to refer that the stem forms of *Europasaurus* + Titanosauriformes node, are based on incomplete specimens such as in *Aragosaurus* or SHN 181.

Lusotitan atalaiensis is placed within Brachiosauridae in a polytomy with *Abydosaurus*, *Giraffatitan*, *Brachiosaurus* and (*Venenosaurus* + (*Tastavinsaurus* + (*Cedarosaurus* + *Sonorasaurus*))) (Fig. 13.2). *Lusotitan* is considered here as a member of Titanosauriformes clade, and this assignation is supported by the presence of swept backwards caudal ribs on anterior caudal vertebrae (#52) and anterior caudal vertebrae dorsoventrally compressed (#287). The resolution within Brachiosauridae is low, being identified a lineage of early cretaceous Laurasian brachiosaurids including *Venenosaurus*, *Tastavinsaurus*, *Cedarosaurus* and *Sonorasaurus*. The placement of *Lusotitan* within Brachiosauridae is supported by the presence of blind fossae on anterior caudal vertebrae (#244); hyposphene ridge on anterior caudal vertebrae (#259) and middle-to-posterior caudal vertebrae dorsoventrally compressed (#288).

13.6. SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842
Saurischia Seeley, 1887
Sauropodomorpha Huene, 1932
Sauropoda Marsh, 1878
Eusauropoda Upchurch, 1995
Turiasauria Royo-Torres et al., 2006
Zby atlanticus Mateus et al., 2014

Holotype: ML 368, a partial skeleton comprising a tooth, an anterior chevron, and a right pectoral girdle and forelimb (an incomplete scapula, coracoid, humerus, radius, ulna, metacarpals I, III, and IV, and manual phalanges I-1, I-2, and ungual phalanx I-2) plus several indeterminate fragments.

Revised diagnosis: *Zby atlanticus* is a turiasaurian sauropod with the following autapomorphies: (1) ulna is arched where the convexity face posteriorly (new, shared with *Cetiosaurus oxoniensis*); (2) a crest in the lateral border of the proximal end of the radius (new); (3) sharp crest along the lateroventral border of the radius diaphysis (new), and (4) manual ungual phalanx I-2 subrectangular in lateral view (Mateus et al., 2014).

Horizon and locality: Vale Pombas (Lourinhã), Portugal, Praia Amoreira–Porto Novo Formation, upper Kimmeridgian-basal Tithonian in age (Manuppella et al., 1999; Mateus, 2005).

Discussion: Mateus et al. (2014) proposed a diagnosis based on four autapomorphies for *Zby atlanticus*: "(1) posteroventral margin of the scapular acromial plate and the anteroventral margin of the blade meet at an abrupt angle (approximately 110º) following a change in slope; (2) humerus expands both anteriorly and posteriorly at the point of the distal half of the deltopectoral crest, as a result of a prominent posterior bulge; (3) laterodistal corner of humerus forms an anteroposteriorly thin flange of bone that does not expand as far anteriorly as the rest of the distal end of the humerus; and (4) manual ungual phalanx I-2 subrectangular in lateral view" (Mateus et al., 2014, p. 619). The redescription of the *Zby atlanticus* holotype (ML368) comparing with other Iberian turiasaurs, in particular, with the holotype of *Turiasaurus riodevensis* (Royo-Torres et al., 2006), *Losillasaurus giganteus* (Casanovas et al., 2001) and the San Lorenzo specimen (Cobos et al., 2011) provide new information about the original diagnosis of *Z. atlanticus*:

- *Scapular acromial plate and the anteroventral margin of the blade meet at an abrupt angle*: The *in situ* observation of the specimens allow us to test the absence of a stepped posteroventral border for the scapular proximal plate of *Zby atlanticus* (Fig. 13.3). Previously pointed out by Mateus (2005), our observations indicate that the most posterior preserved sector of the ventral margin of scapula is broken being impossible to test the presence of a stepped margin for *Zby atlanticus* holotype. In fact, the step observed in the figured scapula of *Zby*, in Mateus et al. (2014), results from a fractured ventral margin (see Fig. 13.3).

- *Presence of prominent posterior bulge*: Mateus et al. (2014) considered as an autapomorphic feature the presence of a lateral bulge on the posterior face of the humeral proximal end (Fig. 13.4). This bulge is interpreted as the attachment site for *M. latissimus dorsi*. In sauropods, this bulge generally appears on the posterior face of the proximal end. As it is referred by Mateus et al. (2014), this bulge is present in some saltasaurids such as *Saltasaurus* (Powell, 1992), *Neuquensaurus* (Otero, 2010) or *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977). In saltasaurids, this tuberosity occupies a more lateral position, being visible in anterior view. However, this type of bulge also appears in other sauropods outside Saltasauridae such as *Cedarosaurus* (Tidwell et al., 1999), *Angolatitan* (Mateus et al., 2011), *Epachthosaurus* (Martínez et al., 2004), *Lirainosaurus* (Díez Díaz et al., 2013) and *Jainosaurus* (Wilson et al., 2011). Outside Titanosauriformes, this tuberosity is not so common, being suggested as autapomorphy of *Zby atlanticus* (Mateus et al., 2014). The direct observation of *Turiasaurus riodevensis* holotype confirms the presence of a similar tuberosity in the posterior face of the humeral proximal end (Fig. 13.4). As in *Z. atlanticus* this tuberosity is not visible in anterior view unlike in saltasaurids (e.g. Powell, 1992; Otero, 2010) and *Cedarosaurus* (Tidwell et al., 1999). Casanovas et al. (2001) also described the presence of a tuberosity on the posterior face of the humeral proximal end of *Losillasaurus*, and the direct observation also confirmed the presence of this bulge. In conclusion, the presence of this tuberosity should not be treated as an autapomorphy of *Z. atlanticus* due presence of a similar tuberosity in other turiasaurian sauropods. A marked attachment site for *M. latissimus dorsi* might be exclusive for turiasaurs within basal eusauropods, and convergent with Titanosauriformes, and so, a putative synapomorphy of Turiasauria.

- *Anteroposterior thin flange on the laterodistal corner of humerus*: This sector of the humerus is not totally preserved in the humerus of the holotype of *Turiasaurus riodevensis*, but some observations and comparisons with other turiasaurs are possible. In *Turiasaurus*, as in *Zby atlanticus*, there is

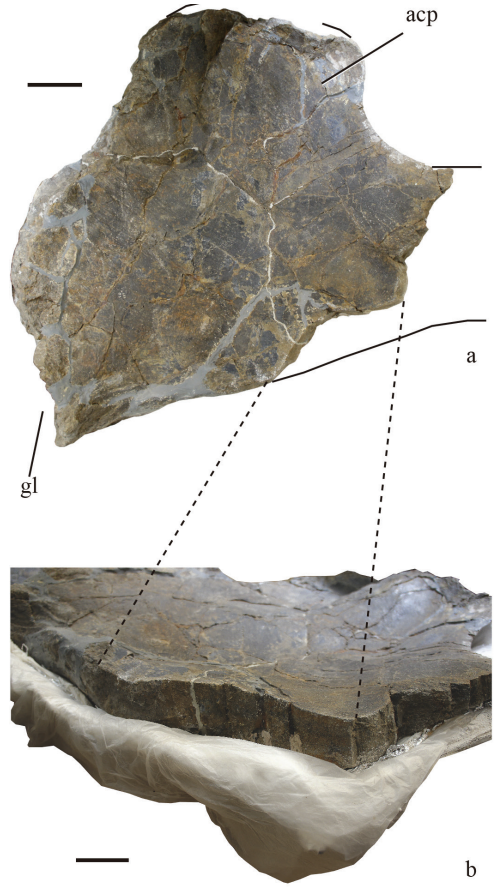

Figure 13.3. Right scapula of *Zby atlanticus*, in medial (a) and ventromedial (b) views. Scale bar = 10 cm.

a thin lamina of bone on the laterodistal corner of the humerus (not previously described) that is distally broken. This thin lamina is bordered anteriorly by a proximodistal groove (Fig. 13.4). The same morphology is observed in *Zby atlanticus* (Fig. 13.4), and described as a laterodistal flange by Mateus et al. (2014). This feature was considered as an autapomorphy of *Zby* by these authors. In conclusion, the presence of a thin flange on the laterodistal corner of humerus presents a wider distribution within Turiasauria and should be excluded from the diagnosis of *Zby atlanticus*. *Losillasaurus* do not bears a lateral crest on the distal end.

- *Manual ungual phalanx I-2 subrectangular in lateral view*: A subrectangular ungual phalanx I-2 (Fig. 13.5) was proposed as diagnostic for *Zby atlanticus* by Mateus et al. (2014). This feature should be treated with caution. In *Turiasaurus riodevensis*, the ungual is not complete and is fractured on the dorsal and distal edge (Fig. 13.5). For *Losillasaurus* no pedal elements are preserved (Casanovas et al., 2001). Comparing the two taxa, no differences are found for the ungual I-2 (Fig. 13.5). In the herein proposed diagnosis of *Zby atlanticus*, the outline of the ungual is included, up to the description of a complete ungual I-2 for other turiasaurian taxon.

Taxonomic status: There are some differences that are recognized between *Zby* and other turiasaurs such as *Turiasaurus* and *Losillasaurus*. One of the proposed autapomorphies of *Turiasaurus* is the presence of anteriorly projected humeral distal condyles, resulting in a concave anterior face of the distal end (Royo-Torres et al., 2006; Royo-Torres and Upchurch, 2012) that are also developed

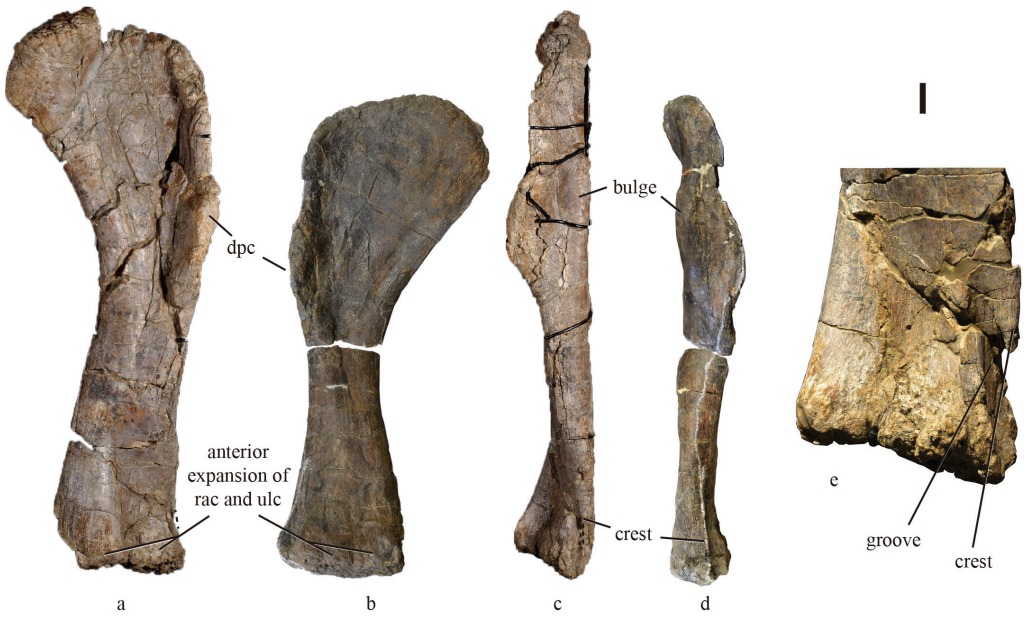

Figure 13.4. Comparison between the humeri of *Turiasaurus riodevensis* and *Zby atlanticus*. Humerus of *Turiasaurus riodevensis* in anterior (a) and lateral (c) views, and anterolateral view of the humeral distal end (e). Humerus of *Zby atlanticus* in anterior (b) and lateral (d) views. Scale bar = 10 cm.

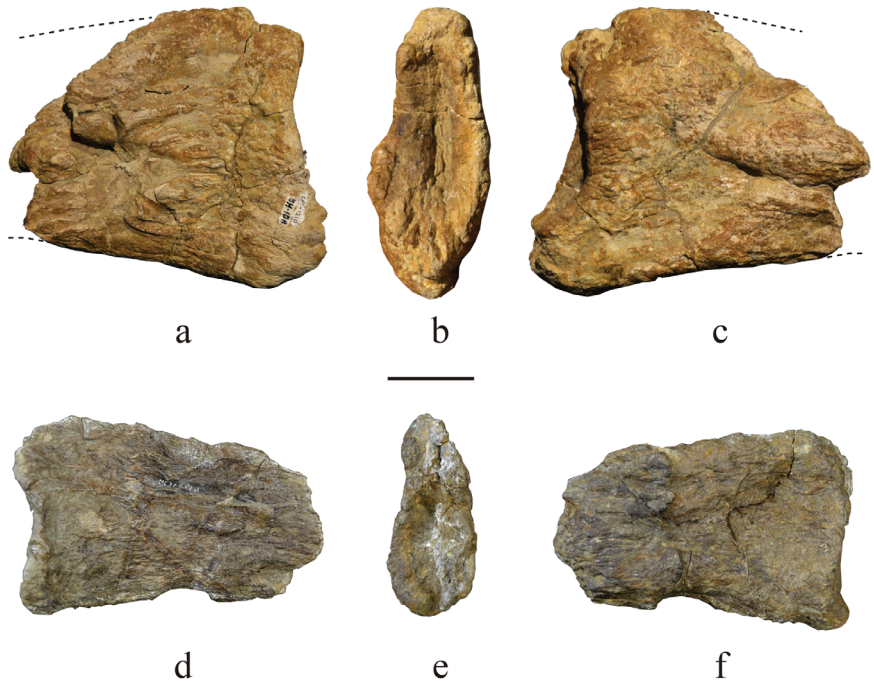

Figure 13.5. Comparison between the unguals I-2 of *Turiasaurus riodevensis* and *Zby atlanticus*. Ungual I-2 of *Turiasaurus riodevensis* in medial (a), proximal (b) and lateral (c) views. Ungual I-2 of *Zby atlanticus* in medial (d), proximal (e) and lateral (f) views. Dashed lines represent extrapolation of the lost bone. Scale bar = 5 cm.

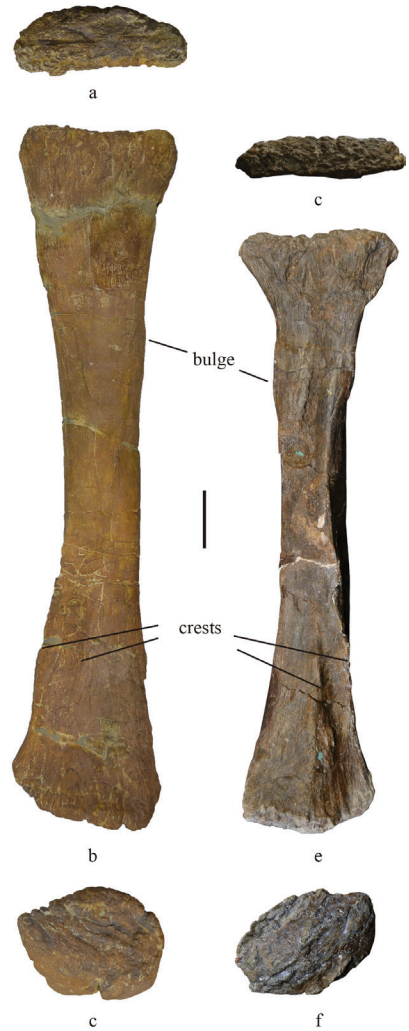

Figure 13.6. Comparison between the radii of *Turiasaurus riodevensis* and *Zby atlanticus*. Radius of *Turiasaurus riodevensis* in proximal (a), posterior (b) and distal (c) views. Radius of *Zby atlanticus* in proximal (a), posterior (b) and distal (c) views. Scale bar = 10 cm.

in other sauropods (e.g. Lehman and Coulson, 2003; Rose, 2007). This feature is not present in *Zby atlanticus*, which present a smooth concave-to-flat anterior face of distal end and not anteriorly projected condyles. The morphology present in *Zby* for the humerus distal end is shared with the *Losillasaurus* holotype.

Other differences are also found between *Zby* and *Turiasaurus*. The reinterpretation of the left radius of *Turiasaurus* allows us to identify several similarities with *Zby atlanticus* (Mateus et al., 2014) (Fig. 13.6). The articular face for the ulna is complex, and *Zby* bears some differences when compared with *Turiasaurus riodevensis* and *Losillasaurus giganteus*. In *Zby*, a proximodistal and sharp crest is present in the lateroposterior border of the radius reaching its proximal part. This feature is considered herein as an autapomorphy of *Z. atlanticus*. Medially to this sharp crest, there are another well-developed, shorter and thicker proximodistal crest. The region between both is transversely concave. This configuration differs in *Turiasaurus*, the lateroposterior and medial crests become distally thick and seem to be associated on the distal end, resulting in a rough bulge.

No well-developed concavity between crests is present as in *Zby*. In *Losillasaurus*, two crests are also present up to the distal end of the radius, nevertheless no deep concavity is present. *Z. atlanticus* also presents a crest in the lateral border of the proximal end that is tentatively proposed as a diagnostic feature of the Portuguese taxon.

Another autapomorphy of *Turiasaurus riodevensis* is a compressed ulnar distal end, resulting in a lacrimal outline in distal view (pointed medioposteriorly). In *Zby atlanticus* the ulnar distal end is subrectangular with a transversely middle constriction (Fig. 13.7). The lateroanterior crest of the distal end is thicker in *T. riodevensis* than in *Z. atlanticus*. The region between the crests for the articulation with the radius bears a more developed concavity in *Z. atlanticus*, visible in distal view. The distal end of *Zby* is not posteromedially projected as occur in *Turiasaurus*, *Losillasaurus* and other sauropods (e.g. Salgado and Bonaparte, 1991; McIntosh et al., 1996a; Allain and Aquesbi, 2008; Carballido et al., 2011; Royo-Torres et al., 2014a; Janensch, 1961). *Zby* also present a general curvature of the ulna where the convexity face posteriorly. This feature is tentatively proposed herein as autapomorphy of *Zby atlanticus*.

In general, the metacarpals of *Turiasaurus riodevensis* show more developed rugosities and rougher surfaces than *Zby atlanticus*. This situation might be a result of different ontogenetic stages as was also pointed out in appendicular bones of *Camarasaurus* (Ikejiri, 2004; Ikejiri et al., 2005) and *Phuwiangosaurus* (Martin, 1994; Martin et al., 1994). The metacarpal I of *Z. atlanticus* shares a similar morphology with that of *T. riodevensis* (Fig. 13.8). In both cases, the lateral condyle of the metacarpal I bears an anteromedial projection. Both taxa also present a markedly rough lateral edge on the distal end (a triangular rough area bordered by two crests). Metacarpal III and IV are also similar in *Z. atlanticus* and *T. riodevensis* showing some smooth differences (Fig. 13.8). In *Z. atlanticus* the distal end of the metacarpal III and IV are more transversely expanded relatively to the diaphysis than in *T. riodevensis*. In lateral view, the metacarpal III of

Figure 13.7. Comparison between ulnae of *Turiasaurus riodevensis* and *Zby atlanticus*. Ulna of *Turiasaurus riodevensis* in proximal (a), posterior (b) and distal (c) views. Ulna of *Zby atlanticus* in proximal (d), anterior (e), posterior (f), lateral (g), medial (h) and distal (i) views. Scale bar = 10 cm.

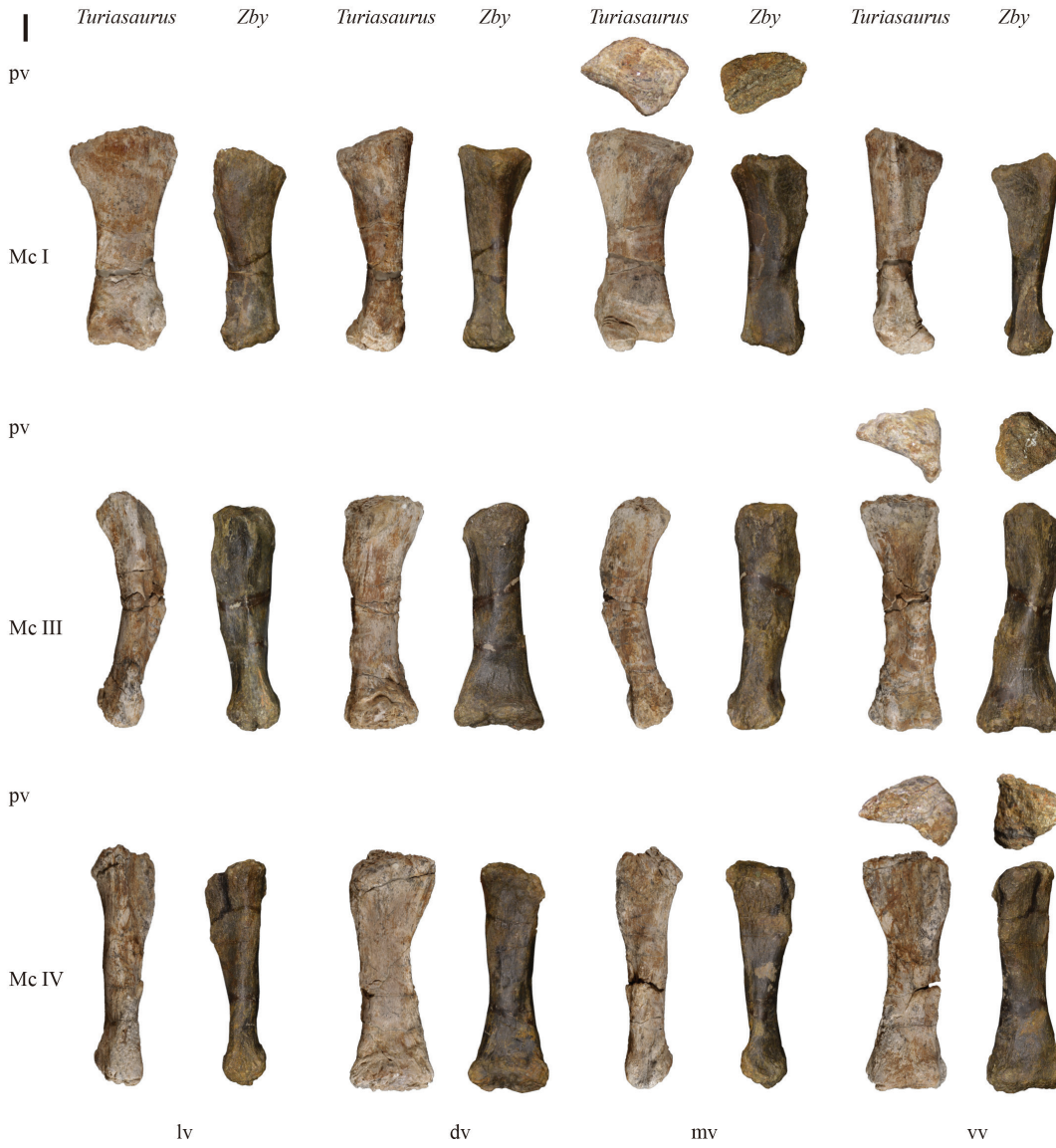

Figure 13.8. Comparison between metacarpal I, III and IV of *Turiasaurus riodevensis* and *Zby atlanticus*. Scale bar equals 5 cm.

T. riodevensis bears more arched profile (with convexity facing posteriorly) and several marked rugosities along the metacarpal. The lateral face of the proximal end is concave and bear a well-marked proximodistal ridge resulting from the articulation with the metacarpal IV. In *Z. atlanticus*, this articulation has a flat surface and lower ridges. The proximodistal crest present in the ventral surface of the metacarpal III for the articulation with the metacarpal IV is visible in proximal view, unlike *Z. atlanticus*. Nevertheless, the proximal surface is not totally preserved in *Zby atlanticus*. Finally, the metacarpal IV is similar for both taxa, differing in the morphology of the proximal end, that is moon-shaped (with concave ventral border) in *T. riodevensis* and subtriangular in *Z. atlanticus*. Also as in the metacarpal III, the proximal end of the metacarpal is not completely preserved in *Z. atlanticus*. In conclusion, some of the differences observed in the morphology of the proximal end might be explained by the presence of some erosion in the *Zby* metacarpals.

Mateus et al. (2014) also pointed out for some differences between *Turiasaurus* and *Zby* based on the absence of: *i*) a well-developed vertical groove on the distal half of the posterior surface of the ulna; *ii*) a strong mediolateral compression of the ulnar distal end; *iii*) dorsolateral bulges near the distal end of metacarpal I. The vertical crests present on the posterior face of *Turiasaurus* ulna distal end (referred by Royo-Torres et al., 2006 and Mateus et al., 2014) are, in fact, the crests for the articulation of the radius (i.e. the posterior face of the ulnar distal end is the anterior side of the ulna). The lacrimal shape of ulnar distal end in *Turiasaurus* is an important difference when compared with the subrectangular morphology presented by *Zby atlanticus* (Fig. 13.7). The dorsolateral bulges of the distal end of the metacarpal I pointed out by Mateus et al. (2014) corresponds to an individualization in two main rough areas of the triangular dorsolateral tuberosity present in both taxa. The morphology of this kind of rugosities in appendicular elements are strongly controlled by the ontogeny as occur in other taxa (Martin, 1994; Martin et al., 1994), and is not considered herein to distinguish *Turiasaurus* from *Zby*.

In conclusion, some differences are identified in *Zby atlanticus* when compared with other turiasaurian sauropods. The detailed comparison between *Zby* and other turiasaurs do not confirm the previously proposed diagnosis (Mateus et al., 2014). Herein, we tentatively propose a new diagnosis for *Zby atlanticus* based on the following exclusive features within Turiasauria clade: (1) the general curvature of the ulna where the convexity face posteriorly; (2) a crest in the lateral border of the proximal end of the radius; and (3) the sharp crest along the lateroventral border of the radius diaphysis.

Eusauropoda Upchurch, 1995
Neosauropoda Bonaparte, 1986
Diplodocoidea Marsh, 1884 (sensu Upchurch 1995)
Flagellicaudata Harris and Dodson, 2004
Diplodocidae Marsh, 1884
Diplodocinae Janensch, 1929 (see Taylor and Naish, 2005)
Diplodocinae indet.

Material: SHN (JJS) 177 is a partial skeleton composed by dorsal (?), sacral and caudal vertebrae, dorsal ribs, chevrons and pelvic girdle elements.

Horizon and locality: Valmitão (Lourinhã, Portugal), Praia Amoreira–Porto Novo Formation, upper Kimmeridgian-basal Tithonian in age (Manuppella et al., 1999).

Comment: SHN (JJS) 177 is one the most complete diplodocine specimens of the Portuguese Upper Jurassic record being composed by several axial elements, including dorsal vertebrae (with doubt), sacral, caudal, dorsal ribs, chevrons and pelvic girdle elements (Mocho et al., 2014b). This specimen is still in preparation but several anatomic aspects might be accessed and encoded. A detailed description will be performed after the full preparation of this specimen, but some anatomical aspects will be discussed bellow. The partial tail, mainly composed by anterior caudal vertebrae, provided us an important amount of information in order to score and discuss the taxonomic affinities of this specimen.

The anterior caudal vertebrae of SHN (JJS) 177 bear the common morphological architecture present in diplodocids and, in particular, in more derived diplodocines (see Osborn, 1899; Hatcher, 1901; Lull, 1919; McIntosh, 2005; Remes, 2006). The available caudal vertebrae present well-developed pleurocoels (they are medially and dorsoventrally deep, and subdivided by several laminae). The presence of developed pleurocoels was considered synapomorphy of Diplodocinae (Wilson, 2002; Carballido et al., 2011; Whitlock, 2011). Tschopp et al. (2005) considered the presence of pleurocoels on anterior-most caudal vertebrae a synapomorphy of Diplodocidae. *Diplodocus*, *Tornieria*, *Barosaurus*, *Dinheirosaurus* and SHN (JJS) 177 bears pleurocoels on non-proximal anterior caudal vertebrae.

The presence of procoelous is also common in diplodocids, and it is considered as a synapomorphy of this clade according the phylogenetic approach of Wilson (2002). On the other hand, the procoelous condition was considered as diagnostic of Diplodocinae (Carballido et al., 2014; Whitlock, 2011).

The diplodocine of Valmitão have well-developed "wing-like" caudal ribs as occur in several other diplodocids (e.g. Osborn, 1899; Hatcher, 1901; Lull, 1919; McIntosh, 2005; Lovelace et al., 2017). Nevertheless, a more precise definition of "wing-like" morphology is needed for future analyses, as was pointed out by Tschopp et al. (2015). Tschopp et al. (2015) considered as synapomorphic of diplodocines a transition from 'fan'-shaped to 'normal' caudal ribs between Cd 6 and Cd 7, or more posteriorly. SHN (JJS) 177 preserves several caudal ribs, suggesting that this morphological transition will probably occur between Cd6 and Cd7, or more posteriorly. Diapophyseal laminae are present in SHN (JJS) 177 caudal vertebrae, feature shared with other diplodocids (synapomorphy of Diplodocidae according Wilson, 2002; Whitlock, 2011; Carballido et al., 2011). This feature was recently proposed as synapomorphy of Flagellicaudata (Tschopp et al., 2015).

The anterior caudal vertebrae are featured by well-developed ventrolateral crests associated with a ventral hollow. This feature is also present in diplodocids, and considered as a synapomorphy of Diplodocinae by Wilson (2002) and Carballido et al. (2011). More recently, Tschopp et al. (2015) considered this feature as diagnostic of Diplodocidae.

The neural arch of the anterior caudal vertebrae bears several important features, which suggest the placement of SHN (JJS) 177 within Diplodocidae. SHN (JJS) 177 has anterior caudal neural arches with sprl-spol contact on lateral aspect of neural spine. This was considered as a synapomorphy of Diplodocidae (Wilson, 2002; Whitlock, 2011; Carballido et al., 2011, Tschopp et al., 2015). Anterior caudal neural spines rectangular in anterior/posterior view were also considered as synapomorphy of Diplodocidae (Whitlock, 2011). These features are shared with several diplodocids such as *Dinheirosaurus* (Mannion et al., 2012; pers. observ., PM and FO, 2014), *Barosaurus* (McIntosh, 2005) and *Diplodocus* (Hatcher, 1901). *Supersaurus* and *Tornieria* differ from more derived diplodocids due the presence of a developed triangular process (Remes, 2006; Lovelace et al., 2007).

Some affinities with more derived diplodocines such as *Barosaurus* or *Diplodocus* are identified in SHN (JJS) 177. Anterior caudal neural spines slightly and distally bifurcate was suggested as synapomorphy of *Barosaurus* + *Diplodocus* clade (Whitlock, 2011) and this feature is present in SHN (JJS) 177 and in the holotype of *Dinheirosaurus lourinhanensis* (pers. observ., PM and FO). Anterior caudal vertebrae with concavo-convex zygapophyseal articulation is considered as synamoporphy of Diplodocinae (Whitlock, 2011) that is also present in *Dinheirosaurus*, *Diplodocus* and *Barosaurus*. In Tschopp et al. (2015) phylogenetic hypothesis, this feature appears several times along the sauropod evolutionary history.

Furthermore, some features present in SHN (JJS) 177 suggest that this form is more closely related to *Diplodocus* than *Barosaurus* (hypothesis supported by the phylogenetic analyses). Tschopp et al. (2015) proposed the presence of a deep ventral hollow on anterior and middle caudal vertebrae (>10mm) as a shared synapomorphy for *Diplodocus carnegii* and *Diplodocus hallorum*. The ventral hollow in SHN (JJS) 177 is extremely deep, suggesting a clear affinity with the genus *Diplodocus*. SHN (JJS) 177 shares with *Diplodocus* the presence of pre-epipophyses on the anterior caudal vertebrae (recovered as synapomorphy of SHN (JJS) 177 + *Diplodocus* in the present analyses), being considered by Tschopp et al. (2015) an autapomorphy of the *Diplodocus* genus. In conclusion, SHN (JJS) 177 bears several features that allow placing it within Diplodocinae, in particular, as a derived form closely related to *Diplodocus*. The full preparation and description of this specimen will allow testing this hypothesis as well as, the possibility of this specimen be distinct of or referable to *Dinheirosaurus lourinhanensis* that still also needs to be fully prepared (see discussion for *Dinheirosaurus*).

Dinheirosaurus Bonaparte and Mateus, 2009
Dinheirosaurus lourinhanensis Bonaparte and Mateus, 2009

1998 *Lourinhasaurus alenquerensis* Dantas et al., 1998
1999 *Dinheirosaurus lourinhanensis* Bonaparte and Mateus, 1999
2003 *Dinheirosaurus lourinhanensis* Antunes and Mateus, 2003
2012 *Dinheirosaurus lourinhanensis* Mannion et al., 2012
2015 *Supersaurus lourinhanensis* Tschopp et al., 2015

Holotype: ML 414, two articulated cervical vertebrae, nine articulated dorsal vertebrae and several neural arch fragments, dorsal ribs, anterior caudal vertebrae and distal fragment of pubis.

Diagnosis: *Dinheirosaurus lourinhanensis* is a diplodocine sauropod that can be diagnosed by the following autapomorphies: (1) the ventral keel is restricted to the posterior portion of the centrum in posterior cervical vertebrae (unique within Flagellicaudata, Tschopp et al., 2015); (2) three small fossae on the lateral face of the neural spine in posterior cervical vertebrae, posterior to the elongated coel (Mannion et al., 2012), (3) dorsal centrum length (excluding articular 'ball') remains approximately the same along the sequence (unique within Diplodocinae; Tschopp et al., 2015).

Horizon and locality: Porto Dinheiro (Lourinhã, Portugal), Praia Amoreira–Porto Novo Formation, upper Kimmeridgian-basal Tithonian in age (Manuppella et al., 1999).

Comments: *Dinheirosaurus lourinhanensis* specimen was recently described in detail by Mannion et al. (2012). These authors provided a revised diagnosis and a new phylogenetic context for this taxon, (mainly based on the dataset of Whitlock, 2011), which suggest that *Dinheirosaurus* is a basal diplodocine, sister taxa of *Supersaurus*. In Mannion et al. (2012) phylogenetic hypothesis, the clade formed by *Dinheirosaurus* + *Supersaurus* is supported by two synapomorphies: i) pleurocoels in middle and posterior dorsal vertebrae divided by a vertical rod-like strut; and ii) an accessory lamina links the posterior centrodiapophyseal lamina (pcdl) and posterior centroparapophyseal lamina (pcpl) in middle and posterior dorsal vertebrae.

The presence of rod-like struts on the pleurocoels of middle and posterior dorsal vertebrae was considered as a synapomorphy of *Dinheirosaurus* + *Supersaurus*. Nevertheless, Tschopp et al. (2015) also pointed out the presence of this feature in apatosaurs. These authors also consider important the full preparation of pleurocoels in order to test the absence or presence of these vertical struts in other diplodocid specimens. This feature was not considered in the data matrix analyzed herein.

Mannion et al. (2012) considered as an accessory lamina a lamina present on the parapophyseal centrodiapophyseal fossa (pacdf) in the 5th and 9th dorsal (but also present in 7th dorsal). They considered this lamina as homologous of a lamina observed in the same fossa on the 3rd dorsal of *Supersaurus*. Furthermore, the phylogenetic analyses of Mannion et al. (2012) retained this feature as a synapomorphy of *Dinheirosaurus* + *Supersaurus*. Nevertheless, the homology between secondary laminae structures within and between taxa is particularly hard to test (see Wilson, 2012). In these taxa, these laminae seem to represent different structures. In the case of *Supersaurus*, this lamina comes from the parapophyses up to the base of the posterior centrodiapophyseal lamina (pcdl), occupying the position of a second posterior centroparapophyseal lamina (pcpl). In *Dinheirosaurus*, this accessory lamina corresponds to the ventral end of the lateral centropostzygapophyseal lamina (lat. cpol) that was intersected by the pcdl and separated from the remaining posterior section of the lat. cpol, as occur in other taxa (e.g. *Diplodocus*, Osborn, 1899). In conclusion, if both laminae are not homologous, the feature proposed by Mannion et al. (2012) should not be considered as synapomorphies of *Dinheirosaurus* + *Supersaurus*.

More recently, in a specimen-level phylogenetic analysis for diplodocids, Tschopp et al. (2015) supported the phylogenetic approach of Mannion et al. (2012), considering *Dinheirosaurus* as sister taxa of *Supersaurus* (and *Austrolodocus* from Tendaguru Formation; Remes, 2007). Furthermore, these authors suggested that the Portuguese taxon might correspond to a species within *Supersaurus*, proposing a new combination, *Supersaurus lourinhanensis*. The *Dinheirosaurus* + *Supersaurus* clade is supported by the following synapomorphies: (1) the ventral surface of middle and posterior cervical vertebrae bears paired pneumatic fossae, separated by a ventral midline keel, (2) the lateral edge of middle and posterior cervical vertebrae, posterior to the parapophysis is marked by a deep groove extending anteroposteriorly along the edge, (3) middle dorsal neural spines bear an oblique accessory lamina that connects the posl to the spol, and (4) dorsal ribs have pneumatopores. However, all synapomophies have a pneumatic origin should be treated with some caution, because they could be related with ontogeny (e.g. Wedel, 2003). The features (2) and (4) are not exclusive within diplodocids (see Tschopp et al., 2015 dataset) but was retained as exclusive for *Supersaurus* + *Dinheirosaurus* within diplodocines on the Tschopp et al. (2015) phylogenetic approach. These two features might represent the plesiomorphic condition within diplodocids, taking into account that they are also present in some apatosaurs. The presence of an oblique accessory lamina that connects the posl with the spol needs to be reevaluated. No true laminae are identified for *Dinheirosaurus* in the region identified by Tschopp et al. (2015, fig. 69). The structure described as a putative lamina might corresponds to the ventral edge of the lateral flat platform present in the summit of the dorsal neural spine as occur in *Diplodocus* (Hatcher, 1901).

Dinheirosaurus lourinhanensis could be distinguished from *Supersaurus vivianae* by the presence of a shallow, anteroposteriorly elongate fossa, located posteroventrally to the pleurocoel on the cervical vertebrae (#126); roughened lateral aspect of prdl on the posterior cervical vertebrae (#153); medially restricted posl on anterior caudal vertebrae (#264); well-developed dorsal bifurcation on anterior caudal neural spines (#267); anterior caudal vertebrae with concavo-convex zygapophyseal articulation (#269).

The directed observation of the *Dinheirosaurus lourinhanensis* type specimen allows recognizing several incongruences in order to its encoding, and that has direct implications on the previously published phylogenetic approaches. *Dinheirosaurus* was previously distinguished from *Diplodocus* and *Barosaurus* by the presence of dorsolateral projected transverse processes and unbifurcated neural spines (e.g. Bonaparte and Mateus, 1999; Mannion et al., 2012). The ventral surface of the dorsal 1 to 5 (*sensu* Mannion et al., 2012) bears two smooth ventrolateral ridges on the centrum that allow to recognize the sagittal plane of these vertebrae, helping on its orientation. Nevertheless, the centra are particular deformed and the neural arches are slightly displaced from the vertebral body (the junction between the neural arch and the centrum is fractured in Dv 3, 4, 5, 7, 8 and 9) being difficult to know the correct position of the neural arch on the centrum. The transverse processes are not complete in Dv 1, 3, 4, 5 avoiding to obtain a precise relationship between the transverse process and neural spine. In Dv 2 the transverse process is mainly laterally directed. In the Dv 7 the distal tip is perpendicular to the neural spine, also suggesting a lateral projection of the transverse process. Herein, the orientation of the transverse process is scored as unknown, waiting for full preparation of the left side that might provide more information about the transverse processes orientation.

Several authors referred that *Dinheirosaurus* has simple dorsal neural spines (Bonaparte and Mateus, 1999; Mannion et al., 2012; Tschopp et al., 2015). The visible sector of the neural spines are transversely compressed, fact that was used in the *Dinheirosaurus* diagnosis and to distinguished it from more derived diplodocines such as *Barosaurus* or *Diplodocus* (Bonaparte and Mateus, 1999; Mannion et al., 2012). The direct observation of the specimen point out that the neural spine assumes a laterodorsal projection, which becomes less pronounce posteriorly.

This situation might be explained by deformation, or by the possibility that these dorsal neural spines be bifurcated. The progressive reorientation of the neural spine to the sagittal plane along the series could be explained by the transition between fully bifurcated neural spines and slightly bifurcated neural spines as occur in *Apatosaurus*, *Diplodocus* or *Barosaurus* (Hatcher, 1901; Lull, 1919; Gilmore, 1936; McIntosh, 2005). When compared with *Barosaurus* or *Diplodocus* dorsal series, the morphological changes observed in *Dinheirosaurus* neural spines morphology are very similar with these taxa, also suggesting the possibility of bifurcation in *Dinheirosaurus*. Until a full preparation, the characters related with the bifurcation of the dorsal neural spines are scored herein as unknown.

The caudal vertebrae on diplodocids are particular diagnostic (see Whitlock, 2011; Tschopp et al., 2015) and an important amount of caudal vertebrae material of *Dinheirosaurus* that belong to the type specimen is still unprepared and cannot be properly described. The direct observation of this material provides important information and allows to verify the presence of convex-concave zygapophyses, transversely concave ventral face with associated ventrolateral ridges, deep pleurocoels, "wing-like" processes, slight procoelous condition, and slight bifurcated neural spines, in particular, a caudal neural spine misidentified as a dorsal neural spine by Mannion et al. (2012, fig. 6). These features suggest a more derived position for *Dinheirosaurus* within Diplodocinae.

Only the full preparation of *Dinheirosaurus* holotype will allow obtaining a precise description for the cervical and dorsal neural spines and for the anterior caudal vertebrae. These elements play an important role in the study of the phylogeny of diplodocines, and the revision of the present *Dinheirosaurus* scoring might introduce important changes in the topology of cladograms of this clade. The present phylogenetic analysis considers *Dinheirosaurus* as a more derived diplodocid than *Supersaurus*, *Tornieria* and *Kaatedocus*. This differs from previous phylogenetic hypotheses (Mannion et al. 2012; Tschopp and Mateus, 2013; and Tschopp et al., 2015), which proposed *Supersaurus* and *Dinheirosaurus* as a monophyletic clade.

In conclusion, the present analysis suggests that *Dinheirosaurus* is a more derived diplodocine than *Supersaurus*, *Kaatedocus* and *Tornieria*, supported by four autapomorphies (see diagnosis) and outside *Supersaurus* genus. The full preparation of the holotype is necessary to provide more information about the phylogenetic context of this taxon within Diplodocinae.

Macronaria Wilson and Sereno, 1998
Camarasauromorpha Salgado et al., 1997
Camarasauromorpha indet.

Material: A single individual (SHN 181) with eight anterior caudal vertebrae (SHN 181/001-008) preserving several neural arches (SHN 181/000 and 009-019), an anterior chevron and a chevron fragment (SHN 181/020-021), right scapula (SHN 181/022) and coracoid (SHN 181/023), a postacetabular process of the left ilium (SHN 181/024-025), two ischia (SHN 181/026-027), two pubis (SHN 181/028-029), a right femur (SHN 181/30), a right tibia (SHN 181/31), a right fibula (SHN 181/32) and a right astragalus (SHN 181/33).

Horizon and locality: Valmitão (Lourinhã, Portugal), Praia Amoreira–Porto Novo Formation, upper Kimmeridgian-basal Tithonian in age (Manuppella et al., 1999).

Comments: The present phylogenetic analysis recovers SHN 181 as a non-titanosauriform macronarian more derived than *Aragosaurus* and more primitive than *Europasaurus*. For a full discussion, see chapter 12.

Camarasauridae Cope, 1877
Lourinhasaurus Dantas et al., 1998
Lourinhasaurus alenquerensis (Lapparent and Zbyszewski, 1957)

1957 *Apatosaurus alenquerensis* Lapparent and Zbyszewski, 1957
1990a ?*Camarasaurus alenquerensis* McIntosh, 1990a
1990b ?*Camarasaurus alenquerensis* McIntosh, 1990b
1996b ?*Camarasaurus alenquerensis* McIntosh et al., 1996b
1998 *Lourinhasaurus alenquerensis* Dantas et al., 1998
2003 *Lourinhasaurus alenquerensis* Antunes and Mateus, 2003

Lectotype: Partial skeleton housed in MG LNEG composed by: cervical vertebrae remains (MG 4956, MG 30373, MG 30377 and MG 30379), twelve dorsal vertebrae and several neurapophyses fragments (MG 4956: 11 dorsal centra; MG 30378: the cranialmost dorsal centra; MG 30384: neurapophyses fragments), several cranial-to-caudal dorsal ribs (MG 30370), five sacral vertebrae (MG 4956), sacral ribs (MG 30380)* and three sacral neural spines (MG 30376)*, three proximal vertebrae and two proximal caudal neurapophyses (MG 4956, MG 30374, MG 30388), chevron fragments (MG 30387)*, left (MG 5780) and right (MG 30371) scapulae, left (MG 5780) and right (MG 30372) coracoids, left (MG 30383) and right (MG 30382) sternal plates*; left (MG 2) and right (MG 30381) humeri, left radius (MG 4979), left ulna (MG 4979), carpal II (MG 30385), left ilium (MG 5781), right (MG 4975) and left (MG 4970) pubis, left and right ischia (MG 4957), left femur (MG 4931), left tibia (MG 4983), left fibula (MG 4984), left astragalus (MG 30375), pedal (?) phalanx 2 (MG 30386)* and other several indeterminate fragments without explicit acronyms. All these elements are labeled and related with a unique individual, but some elements (marked with asterisk) were not explicitly referred in the original description (Lapparent and Zbyszewski, 1957); and there are some elements, originally quoted by these authors that cannot be recognized in the available set of elements.

Diagnosis: Macronarian having the following autapomorphies: (1) cranial-to-middle dorsal vertebrae with transversely concave ventral face bounded by longitudinal smooth crests; (2) sagittal keel in dorsal margin of sacral neural spines; (3) when the sacral neural spines are vertical, they become significantly higher posteriorly, and the dorsal margin bears a marked anterior slope; (4) prespinal process with a sagittal lamina (prespinal lamina) in the dorsal sector of the sacral spine dividing a smooth prespinal fossa; (5) circular and deep spinoprezygapophyseal fossa on anterior caudals (shared by Jobaria); (6) the dorsal surface of the most anterior caudal spine slopes anteriorly transiting continuously to the anterior face of the spine, and the posterior edge produces a transverse hooked-like process in lateral view; (7) circular process on distal surface of carpal II; (8) longitudinal crest in ventral margin postacetabular process of the ilium near ischiatic peduncle; (9) posterior orientation of the postacetabular process with the chord through the ischiatic and pubic articulations passing through ventral margin of the postacetabular process; (10) axis of pubic peduncle and ischiatic articulation parallelized; (11) marked crest and groove bordered the lateral margin of acetabulum in the ischium; (12) tibia and fibula with equal length, implying a more distal position of the fibula relatively to the tibia for the reception of the astragalus; (13) a marked deflection of the entire femoral shaft without lateral bulge.

Horizon and locality: Moinho do Carmo, Alenquer municipality, northern of Lisboa, Sobral Formation (or Sobral Member of Farta Pão Formation sensu Schneider et al., 2009), upper Kimmeridgian-lower Tithonian, Lusitanian Basin.

Comments: The present phylogenetic analysis recovers *Lourinhasaurus* as a member of Camarasauridae. For a full discussion see Mocho et al. (2014a) or the chapter 10.

Titanosauriformes Salgado et al., 1997
Brachiosauridae Riggs, 1904 (sensu Wilson and Sereno, 1998)
Lusotitan Antunes and Mateus, 2003
Lusotitan atalaiensis (Lapparent and Zbyszewski, 1957)

1957 *Brachiosaurus atalaiensis* Lapparent and Zbyszewski, 1957
2003 *Lusotitan atalaiensis* Antunes and Mateus, 2003
2013 *Lusotitan atalaiensis* Mannion et al., 2013a

Lectotype: The type material corresponds to a unique individual and are composed by a middle-to-posterior dorsal vertebrae (MG 4985-1), a dorsal transverse process (MG 8809), dorsal rib fragments (MG 5795, MG 8793), one sacral vertebra (MG 4801), two sacral spines (an unlabeled sacral neural spine and MG 8807), one sacral rib (MG 4798), 19 caudal vertebrae (MG 4985 2-20), several chevrons arches (an unlabeled anterior chevron and MG 4805-10); left (MG 4944) and right (MG 4989) humeri, left ulna (MG 4966), left (MG 4950) and right (MG 4958) radius; one pubis (MG 4965), one ischium (MG 4952), left tibia (MG4981), left fibula (MG 4982), and the left astragalus (MG 4803). It also identified several fragments (MG 8794, 4838) including a plate-like previously assigned to the ilium (MG 4838), considered here has an indeterminate fragment, and other indeterminate fragments (MG 3794).

Revised diagnosis: *Lusotitan* is a brachiosaurid with the following autapomorphies (*exclusive of *Lusotitan*): (1) spdl does not reach the distal process on sacral neural spines*; (2) small lateral projection of spol at midheight of the most anterior sacral spine*; (3) the caudal rib on the anteriormost caudal vertebra is convex dorsolaterally in posterior view (*sensu* Mannion et al., 2013); (4) anterior-to-middle caudal postzygapophyses transversely compressed, constituting elongate processes that project well beyond the posterior margin of the neural arch (*sensu* Mannion et al., 2013); (5) the presence of transverse elongated or T-shaped pits in the middle caudal vertebrae* (modified from Mannion et al., 2013); (6) circular fossae in the ventral face of the middle caudals, anteriorly located to the chevron facets (new); (7) presence of proximal bridged chevrons (new); (8) short ischiatic peduncle (new); (9) pubis blade with a marked anterior orientation (new); (10) anterior margin of pubis peduncle bearing a rounded projection (new); (11) pubis peduncle of the ischium constricted in anterior view* (new); (12) tibia strongly bowed laterally (*sensu* Mannion et al., 2013); (13) no vertical groove extending up the shaft between the lateral and medial malleoli of the tibia (*sensu* Mannion et al., 2013); (14) tibial crest ventrally directed* (new); (15) acute lateral margin of the tibia, bordered by dorsoventral smooth grooves (new); (16) abrupt transition between the dorsal surface of the articular surface of ascending process and the lateral surface of the tibial shaft* (new).

Locality and horizon: Peralta, near Atalaia locality on Lourinhã municipality, northeast of Lisboa. Sobral Formation, upper Kimmeridgian-lower Tithonian, Lusitanian Basin (Manuppella et al., 1999).

Comments: The present phylogenetic analysis recovers *Lusotitan* as a member of Brachiosauridae. For a full discussion see chapter 11.

13.7. PORTUGUESE UPPER JURASSIC SAUROPODS IN THE CONTEXT OF THE PERI-NORTH ATLANTIC AREA

The present analysis proposes a new phylogenetic approach for Portuguese Upper Jurassic sauropods in order to improve and test the last contributions about their evolutionary history. Recent works have been suggesting that the sauropods of the Lusitanian Basin Upper Jurassic are represented by endemic genera (Dantas et al., 1998; Bonaparte and Mateus, 1999; Antunes and Mateus, 2003; Mateus et al., 2014) closely related to groups present in other continents during the Upper Jurassic such as brachiosaurids (Antunes and Mateus, 2003; Mannion et al.,

2013a), diplodocids (Bonaparte and Mateus, 1999; Mannion et al., 2012; Mocho et al., 2014b) or camarasaurids (Mocho et al., 2014a). The supposed close relationship of the Portuguese sauropods with taxa from the North American Upper Jurassic of the Morrison Formation (e.g. Lapparent and Zbyszewski, 1957; Tschopp et al., 2015) is less close than it is interpreted in other dinosaur groups. In fact, there are references to genera and even species of theropods, ornithopods and stegosaurs (Galton, 1980; Pérez-Moreno et al., 1999; Mateus and Antunes, 2000a, b; Ortega et al., 2006, 2009; Mateus et al., 2006; Escaso et al., 2007, 2010; Malafaia et al., 2007, 2010, 2015; Hendrickx and Mateus, 2014), plants (Mohr, 1989), mammals (Martin, 2000), and ostracods (Schudack, 2000) with an amphiatlantic distribution.

The developed analysis integrates Upper Jurassic forms in order the test the relationships of the Portuguese sauropods among them, with the sauropod faunas of Europe (e.g. Villar del Arzobispo Formation), North America (Morrison Fm.), South America (Cañadón Calcáreo Fm.) and Africa (Tendaguru Fm.), and in the sauropod context. The present analysis recovered the presence of four main lineages in the Portuguese Upper Jurassic record: turiasaurs, diplodocines, camarasaurids and brachiosaurids, and a basal macronarian as a stem member of the Titanosauriformes.

Diplodocinae is a clade within Diplodocidae that includes all taxa more closely related to *Diplodocus* than to *Apatosaurus* (stem-based; Taylor and Naish, 2005). Its known fossil record shows a short stratigraphic range: from the Upper Jurassic to the upper Berriasian-Valanginian, as well as a wide paleogeographic spread during the Upper Jurassic, being present in North America, Europe and Africa, i.e., with a Laurasian and Gondwanan distribution (e.g. Upchurch et al., 2004; Whitlock, 2011; Gallina et al., 2014; Tschopp et al., 2015) (Fig. 13.9, 13.10). The first doubtless diplodocine evidence in the European Upper Jurassic was *Dinheirosaurus lourinhanensis* holotype (Bonaparte and Mateus, 1999). Several phylogenetic analyses confirm that *Dinheirosaurus* corresponds to a diplodocid diplodocine (Rauhut et al., 2005; Whitlock, 2011; Mannion et al., 2012; Tschopp and Mateus, 2013; Tschopp et al., 2015). Several other occurrences were reported for this clade in the Iberian Upper Jurassic (Royo-Torres et al., 2009; Mannion et al., 2012; Mocho et al., 2014b) suggested that this group was relatively abundant in this territory during the Kimmeridgian-lower Berriasian. Nevertheless, the paleobiodiverstiy of this group on the Iberian territory still remains unclear, up to the full preparation and description of several important specimens, such as *Dinheirosaurus* holotype (ML 414, Mannion et al., 2012, pers. observ., PM) and SHN (JJS) 177, 178 and 179 (Mocho et al., 2014b). The present analysis recovers *Dinheirosaurus* and SHN (JJS) 177 as derived diplodocines, more derived than *Supersaurus*, *Tornieria* and *Kaatedocus*. In particular, SHN (JJS) 177 corresponds to a closely related form to *Diplodocus*, a diplodocine from the Upper Jurassic Morrison Formation (Fig. 13.9).

Considering the present analyses, and the most recent phylogenetic approaches for this group of sauropods (Whitlock, 2011; Mannion et al., 2012; Tschopp and Mateus, 2013; Gallina et al., 2014; Tschopp et al., 2015), diplodocines were able to disperse between the Laurasian and the Gondwanan territory before the Kimmeridgian (≈157 m.a.) (Fig. 13.9). In particular, the most derived diplodocines seem to be exclusive from Laurasia, including forms such as *Dinheirosaurus*, *Diplodocus* and *Barosaurus*. Apatosaurinae is exclusive of North America, but there are some occurrences with putative apatosaur affinities in Iberian Peninsula (Suñer et al., 2014) probably indicating a wider distribution for this group in Laurasia. In the present analysis and in the Tschopp et al. (2015) phylogenetic approach, Gondwanan diplodocines occupy a relative basal position within Diplodocinae. For the moment, the Portuguese Upper Jurassic diplodocines present clear affinities with the more derived forms from the Morrison Formation such as *Barosaurus* and *Diplodocus*.

Other group with a wide paleobiogeographic range in the Upper Jurassic is Camarasauridae. The camarasaurids are relatively abundant in Upper Jurassic sediments of the Morrison Formation (Osborn and Mook, 1921; Ostrom and McIntosh, 1966; Madsen et al., 1995;

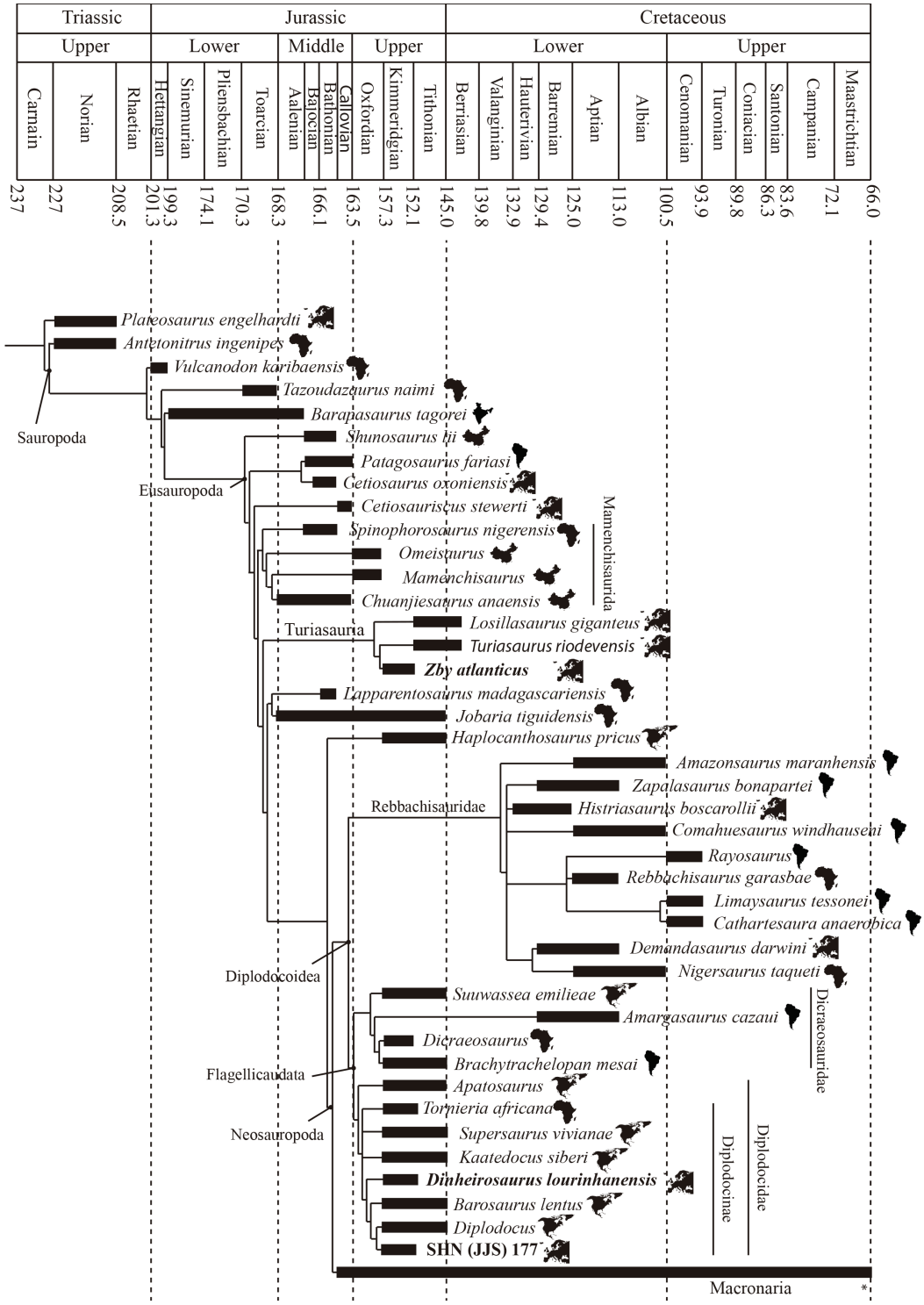

Figure 13.9. The time-calibrated (following Cohen et al., 2013, updated) strict consensus of 384 MPTs of 1508 steps with a consistency index (CI) of 0.351 and a retention index (RI) of 0.755 through time. The present cladogram only includes the non-macronarian sauropods.

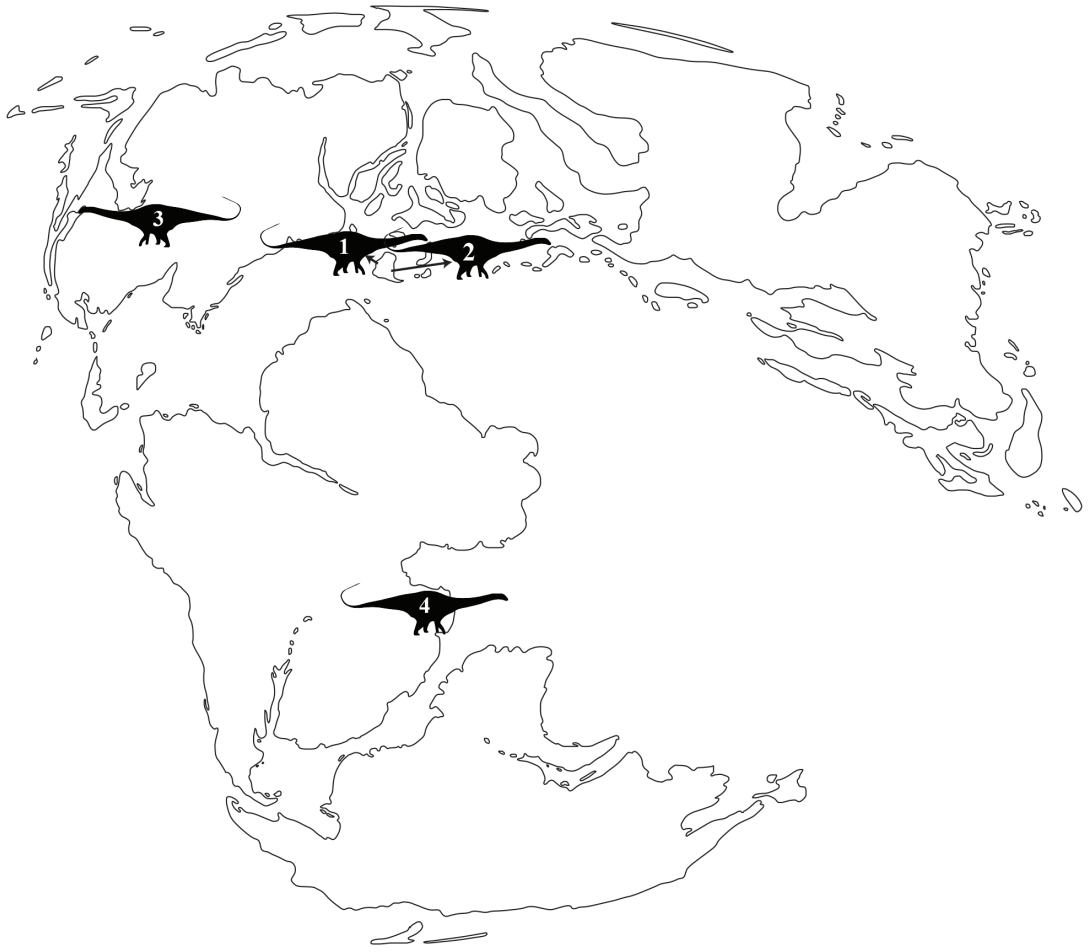

Figure 13.10. Paleobiogeographic distribution of diplodocines during the Upper Jurassic (paleogeographic map modified from Ron Blakey, Colorado Plateau Geosystems). 1- *Dinheirosaurus lourinhanensis*; 2- diplodocine material found in the Villar del Arzobispo; 3- Morrison dipodocines such as *Diplodocus* or *Barosaurus*; 4- *Tornieiria*.

McIntosh et al., 1996a, b; Ikejiri, 2004; Ikejiri et al., 2005) and they are also present in the Upper Jurassic of the Lusitanian Basin (Portugal) with the genus *Lourinhasaurus* (Mocho et al., 2014a) (Figs. 13.11, 13.12, 13.13). Furthermore, some new specimens present important affinities with the Morrison Fm. forms, in particular, a specimen from Cambelas (Torres Vedras, SHN 531) with axial and appendicular elements (Mocho et al., 2013a, b). In the present analysis and in Mocho et al. (2014a) phylogenetic approach, *Tehuelchesaurus* is considered as a basal camarasaurid, suggesting that this group is also represented in the South American Upper Jurassic (Figs. 13.11, 13.12, 13.13). Nevertheless, it is important to consider that the Bremer supports and bootstrap values are relatively low in the base of Camarasauridae but significant for *Camarasaurus* + *Lourinhasaurus* node (Fig. 13.2). As in the case of diplodocines, camarasaurids might be able to disperse between the Laurasian and the Gondwanan territory before the Kimmeridgian age.

Brachiosauridae is another clade also present in Laurasia and Gondwana, with forms in North-America, Europe and Africa (e.g. Upchurch et al., 2004; Rauhut et al., 2006; D'Emic, 2012; Mannion et al., 2013a) (Figs. 13.11, 13.12, 13.14). The resolution of Brachiosauridae in our phylogenetic approach is lower, being difficult to obtain a clear scenario for the phylogenetic

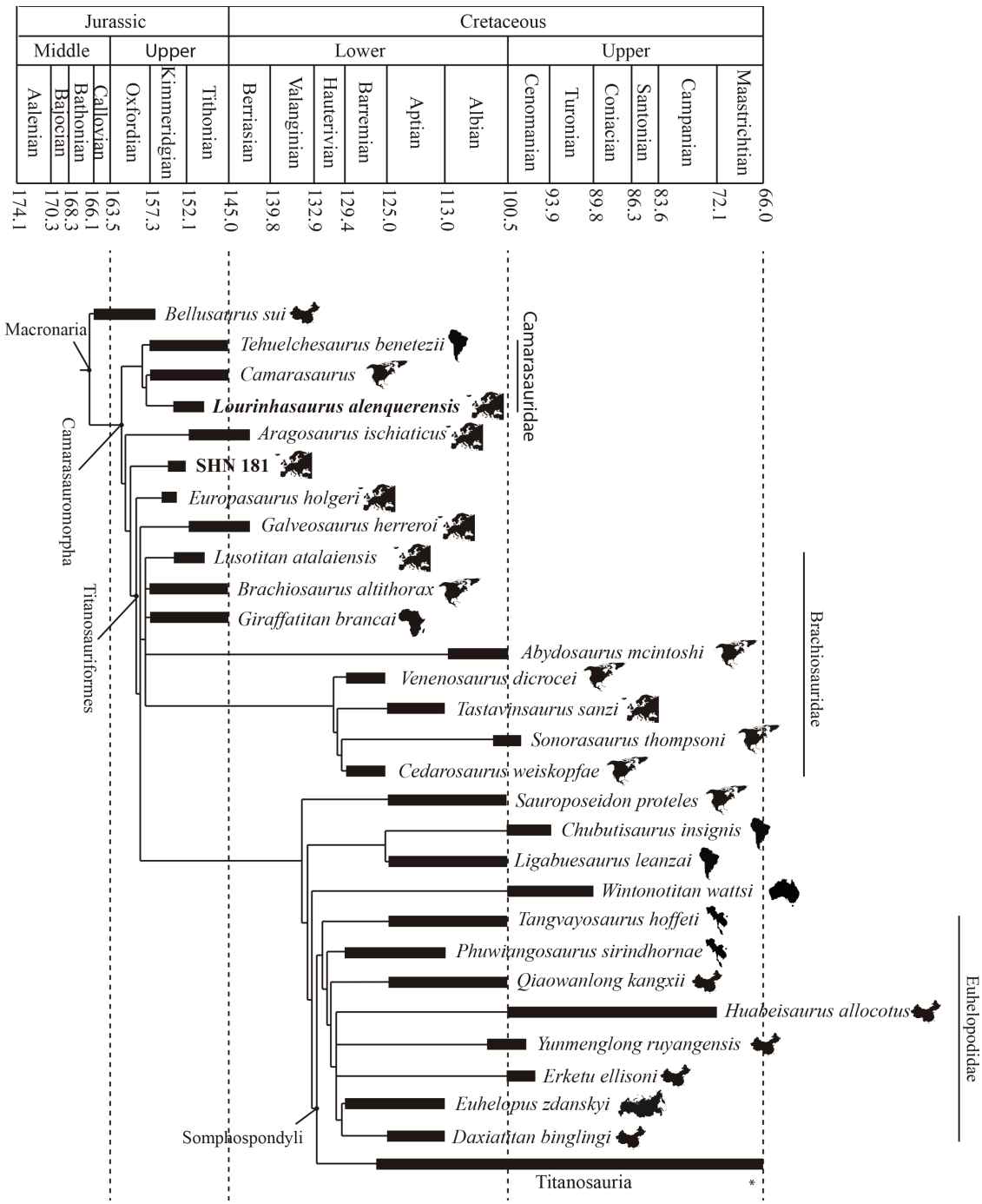

Figure 13.11. The time-calibrated (following Cohen et al., 2013, updated) strict consensus of 384 MPTs of 1508 steps with a consistency index (CI) of 0.351 and a retention index (RI) of 0.755. The present cladogram only includes macronarian sauropods (titanosaurs in figure 13.12).

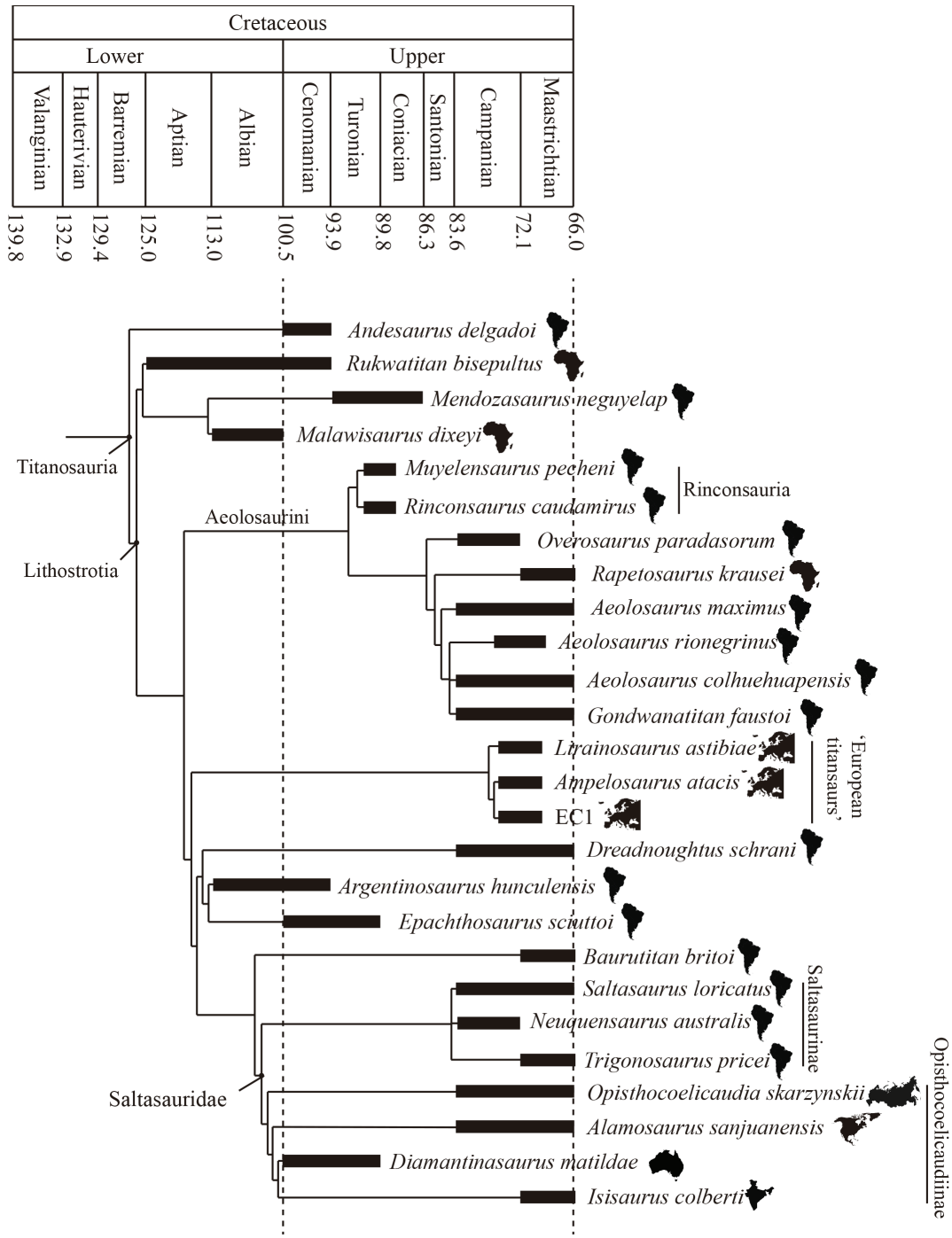

Figure 13.12. The time-calibrated (following Cohen et al., 2013, updated) strict consensus of 384 MPTs of 1508 steps with a consistency index (CI) of 0.351 and a retention index (RI) of 0.755 through time. The present cladogram only includes macronarian sauropods (non-titanosaur macronarians in figure 13.11).

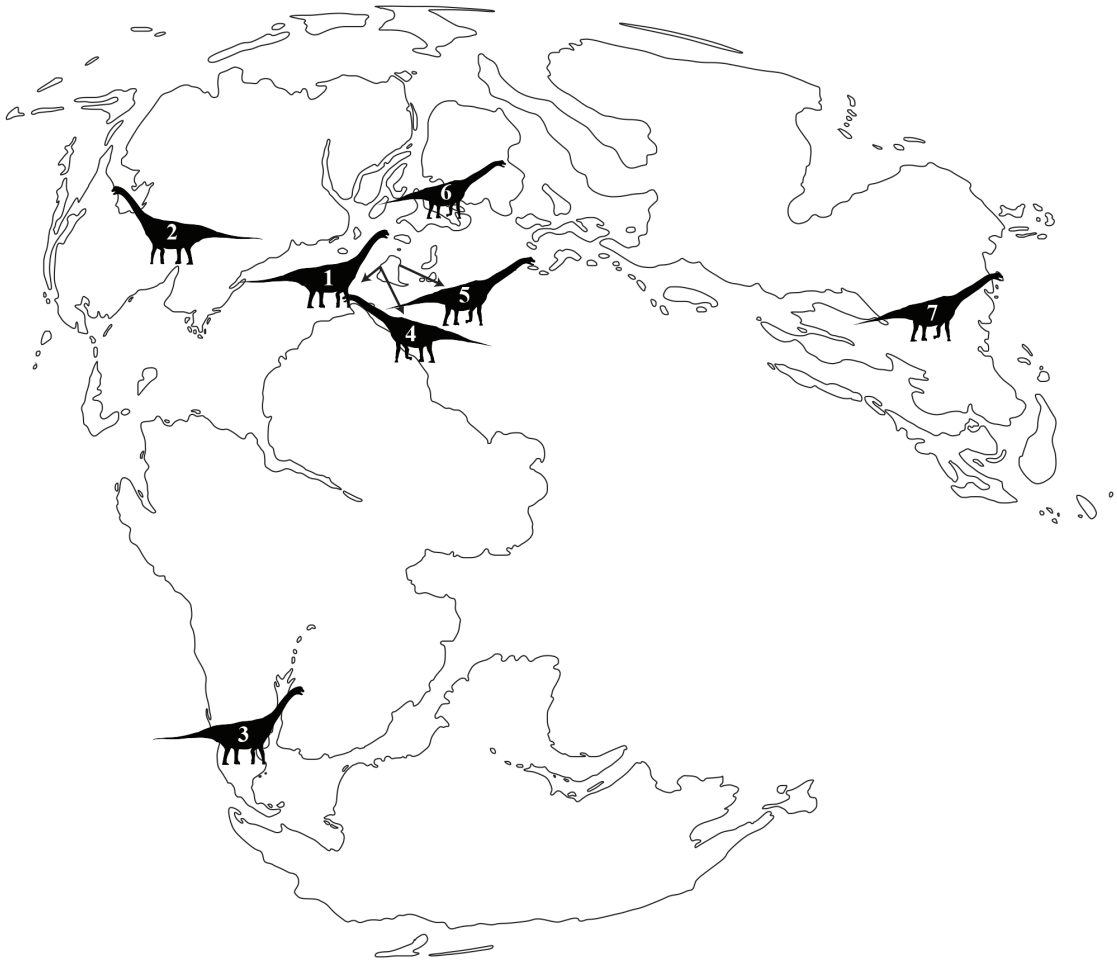

Figure 13.13. Paleobiogeographic distribution of camarasaurids and other basal macronarians during the Upper Jurassic (modified from). 1- *Lourinhasaurus*; 2- *Camarasaurus*; 3- *Tehuelchesaurus*; 4- SHN 181; 5- *Aragosaurus*; 6- *Europasaurus*; 7- *Bellusaurus*.

relationships between them (Fig. 13.2). In the present analysis, a group of Lower Cretaceous brachiosaurids is supported, including four Laurasian forms, *Tastavinsaurus*, *Venenosaurus*, *Sonorasaurus* and *Cedarosaurus* (Figs. 13.11, 13.12). This group is recovered in polytomy with *Brachiosaurus*, *Abydosaurus*, *Giraffatitan* and *Lusotitan*. The systematic revision of the putative brachiosaurid from Damparis (France, Lapparent, 1943) will be important to understand the diversity of this clade in Europe, and understand the affinities of *Lusotitan* with other Laurasian brachiosaurids. A systematic framework focused in brachiosaurids is also necessary to understand the evolution of this clade during the Upper Jurassic. *Galveosaurus* is another form that was considered as a putative brachiosaurid (D'Emic, 2012) and is recovered herein as basal titanosauriform. Furthermore, the comparison between this taxon and *Lusotitan* lectotype suggests that *Galveosaurus* might represents a junior synonymous of *Lusotitan atalaiensis* (see Chapter 11). The redescription of *Galveosaurus* type material will support or refute this hypothesis.

Zby atlanticus is another form of the Portuguese Upper Jurassic. *Zby* is related with Turiasauria, a non-neosauropod eusauropod group. The phylogeny of non-Asiatic basal eusauropods of the Upper Jurassic is uncertain and they seem to be represented in North America, Europe and

Africa (Figs. 13.11, 13.15). In the North-American realm (Fig. 13.15), non-neosauropods are possible represented by *Haplocanthosaurus* comprising two species: *H. priscus* Hatcher, 1903 and *H. delfsi* McIntosh and Williams, 1988. Nevertheless, the phylogenetic position of *Haplocanthosaurus* is uncertain, being recovered as a basal macronarian in some phylogenetic hypotheses (e.g. Wilson and Sereno, 1998; Upchurch et al., 2004; Royo-Torres et al., 2006; Carballido and Sander, 2014), a basal diplodocoid (e.g. Wilson, 2002; Remes, 2006; Remes et al., 2009; Royo-Torres et al., 2009, 2012; Whitlock, 2011; Royo-Torres and Upchurch, 2012) or a non-neosauropod (e.g. Harris, 2006). Furthermore, Calvo and Salgado (1995) suggested that *Haplocanthosaurus* could be paraphyletic, with *H. priscus* more related to Diplodocoidea. Herein, *H. priscus* is considered as non-neosauropod eusauropod more derived than turiasaurian sauropods.

The phylogenetic context for some Tendaguru taxa is uncertain, in particular, *Janenschia*, *Tendaguria* and HMN MB.R.2091.1-30. They might represent non-neosauropod eusauropods. Some authors suggested HMN MB.R. 2091.1-30 as a putative mamenchisaurid (Mannion et al., 2013a; 2013b)

Figure 13.14. Paleobiogeographic distribution of titanosauriforms during the Upper Jurassic (paleogeographic map modified from Ron Blakey, Colorado Plateau Geosystems). 1- *Lusotitan*; 2- sauropod of Damparis (Lapparent, 1943); 3- *Brachiosaurus*; 4- *Giraffatitan*; 5- brachiosaurid skeleton MPEF PV 3099 (locality DD 02) in the Cañadón Calcáreo Formation of Chubut (Argentina, Rauhut, 2006); 6- *Brachiosaurus* sp. Kadzi Formation (unspecified Late Jurassic, Raath and McIntosh, 1987); 7- *Galveosaurus*.

Figure 13.15. Paleobiogeographic distribution of non-neosauropod eusauropods during the Upper Jurassic (paleogeographic map modified from Ron Blakey, Colorado Plateau Geosystems). 1- *Zby*; 2- *Turiasaurus*; 3- *Losillasaurus*; 4- *Haplocanthosaurus*; 5- *Jobaria* (age in doubt); 6- *Janenschia* and *Tendaguria* (uncertain phylogeny); 7- mamenchisaurids; 8- HMN MB.R.2091.1-30.

by the presence of anterolaterally projected caudal ribs and procoelous centra. If Mannion et al. (2013a, b) hypothesis is correct; this will be one of the first mamenchisaurid occurrences outside Asia. According with our analysis, *Spinophorosaurus nigerensis* from the Middle Jurassic of Niger (Remes et al., 2009) might represent a basal mamenchisaurid, suggesting that this group had a more widespread paleobiogeographic distribution during the Middle Jurassic than previous though. This might explain the presence of a mamenchisaurid form on the Upper Jurassic of Tendaguru Beds without consider an Upper Jurassic contact between African and Asiatic faunas. *Janenschia* is a problematic taxon and the type specimen might represent different types of sauropods (Bonaparte et al., 2000; Royo-Torres and Cobos, 2009). It was considered as a basal macronarian (e.g. Bonaparte et al., 2000; Carballido et al., 2011; Mannion et al., 2013a) or a basal titanosauriform (D'Emic, 2012). The tail of HMN MB.R. 2091.1-30 was originally referred to *Janenschia* and several authors related this taxon to Titanosauria clade (e.g. Janensch, 1929; Upchurch, 1995; Wilson and Sereno, 1998; Upchurch et al., 2004; Curry Rogers, 2005; Mannion and Calvo, 2011). *Tendaguria* was considered as a Sauropoda *incertae sedis* (Bonaparte

et al., 2000; Upchurch et al., 2004), a possible titanosaur (Mannion and Calvo, 2011), a non-neosauropod (Carballido et al., 2011; Mannion et al., 2013b), a basal macronarian (Carballido et al., 2011), a basal titanosauriform (Carballido and Sander, 2014), a sister taxa of Neosauropoda or a basal diplodocoid (Mannion et al., 2013a). Royo-Torres and Cobos (2009) and Royo-Torres et al. (2014b) related to Turiasauria some specimens found in Tendaguru Fm. such as a complete right manus (HMN MB.R.2093.1-12), a partial caudal series described by Bonaparte (2000, HMN MB. R.2091.1-30), an astragalus (HMN B.R.2095.6) and a humerus (HMN MB.R.2910). A full phylogenetic reassessment of this material and the discovery of more specimens referable to these enigmatic taxa will be important to obtain a more complete systematic context. For the moment, any phylogenetic and paleobiogeographic inference will be probably premature and weak supported.

The non-neosauropod eusauropods are well represented in the Upper Jurassic fossil record of the Iberian Peninsula, with several turiasaurian specimens, and three established taxa, *Turiasaurus riodevensis* (Royo-Torres et al., 2006), *Losillasaurus giganteus* (Casanovas et al., 2001) and *Zby atlanticus* (Mateus et al., 2014). As it was referred above, Royo-Torres and Cobos (2009) and Royo-Torres et al. (2014b) noted for the presence of this clade on the Upper Jurassic of Tanzania (Africa), nevertheless, this hypothesis still needs to be confirmed based on phylogenetic analyses as suggested Mannion et al. (2013a). Not considering the putative Upper Jurassic turiasaurian remains of Africa, Turiasauria clade is restricted to the Iberian territory during this period, and the hypothesis of endemicity for this clade is not ruled out. More recently, *Atlasaurus* have been considered as member of the Turiasauria clade (Royo-Torres et al., 2014b; Xing et al., 2015), suggesting a more wide stratigraphic and paleobiogeographic distribution for turiasaurs during the Middle Jurassic. New discoveries as well as the systematic revision of *Turiasaurus riodevensis* and *Losillasaurus giganteus* will shed light in the paleobiographic context of turiasaurs.

The proposed phylogenetic approach also considers the presence of several basal macronarians more derived than Camarasauridae and more primitive than Titanosauriformes in the European Upper Jurassic record such as *Aragosaurus*, *Europasaurus*, SHN 181 and *Galveosaurus* (that might represent a basal titanosauriform). *Aragosaurus* was considered a camarasaurid and was originally dated as probably Hauterivian? (Sanz et al., 1987) or Valanginian?-Hauterivian age (Canudo et al., 2012). Nevertheless, some authors proposed a Tithonian–Berriasian age for *Aragosaurus* (Alcalá et al., 2009; Royo-Torres et al., 2009, 2014a; Cobos and Gascó, 2013). The full description of the type specimen allowed to propose a new phylogenetic context, considering it as a basal macronarian more derived than Camarasauridae and more primitive than *Europasaurus* + Titanosauriformes (Royo-Torres et al., 2014a), as is also supported by the present analysis (Fig. 13.2). SHN 181 presents several similarities with *Aragosaurus*, but the presence of several apomorphies justify a more derived position. The European Upper Jurassic basal macronarians are relatively unknown and incomplete outside the Iberian Peninsula. The exception is the German taxon, *Europasaurus holgeri* (Sander et al., 2006; Carballido and Sander, 2014; Marpmann et al., 2015). *Europasaurus* was considered as a member of Brachiosauridae (D'Emic, 2012; Mannion et al., 2013a) or as a non-titanosauriform macronarian (Carballido et al., 2011; Carballido and Sander, 2014; Royo-Torres et al., 2014).

This analysis suggests a wide distribution for the main lineages recorded in the Portuguese Upper Jurassic, being present in Europe, North America and Africa, and South America in the case of the camarasaurids. This distribution along Laurasia and Gondwana suggests for faunal contact between these territories before Kimmeridgian. The contact between North America and Iberian Peninsula faunas have been explained by a temporary short-duration regional uplift around the Callovian/Oxfordian transition (≈163.5 M.a., Mateus et al., 2013) or by an episodic "Newfoundland-Iberia" faunal corridor during the uppermost Kimmeridgian–lowermost Tithonian

(≈148-153 M.a., Escaso et al., 2007). The neosauropod lineages recorded in North America, South America, Europe and Africa are so far absent in Asia, with the exception of *Bellusaurus* (Dong, 1990). *Bellusaurus* was recently recovered as a basal macronarian (e.g., Royo-Torres et al., 2006; Carballido and Sander, 2014; this analysis), suggesting the presence of this group during the Late Jurassic in East Asia. If eusauropod non-neosauropod placement of *Bellusaurus* is supported, no other neosauropod is recognized in East Asia territory during the Late Jurassic. The absence of neosauropods in East Asia during the Late Jurassic agreed with the proposed isolation of this territory at the Middle Jurassic to Lower Cretaceous boundary, resulting in the development of endemic faunas composed by non-neosauropod eusauropods (e.g. Milner and Norman, 1984; Upchurch, 1995; Barrett et al., 2002; Wilson and Upchurch, 2009).

In conclusion, the Upper Jurassic sauropod faunas from the Lusitanian Basin are mainly composed by turiasaurs, diplodocines, camarasaurids, non-titanosauriforms macronarians and brachiosaurids. This analysis also confirm the presence of exclusive taxa for the Portuguese Upper Jurassic record, some of them with clear affinities with the North-American forms, situation also observed for other dinosaurs (Hendrickx and Mateus, 2014; Escaso et al., 2014) that might results from processes of incipient vicariance after a faunal contact. The diplodocine and camarasaurid forms described for the Portuguese Upper Jurassic are more closely related to the Morrison forms than to the Gondwanan representatives of the group. This could be a consequence of a common history close in time among these territories. The phylogenetic affinities of the Portuguese Upper Jurassic brachiosaurids remain unclear resulting from a low resolution within Brachiosauridae clade. Turiasauria is non-neosauropod eusauropod clade well represented in the Iberian territory, composed by three established taxa, *Turiasaurus*, *Losillasaurus* and *Zby*. In the Spanish Upper Jurassic, the Villar del Arzobispo sauropod faunas are also composed by turiasaurs, diplodocines and non-titanosauriform basal macronarians. No particular differences are found between Portuguese and Spanish Upper Jurassic sauropod faunas.

13.8. CONCLUSIONS

A new phylogenetic approach is presented for Portuguese Upper Jurassic sauropods. The phylogenetic analysis includes for the first time all Portuguese taxa (*Lourinhasaurus*, *Dinheirosaurus*, *Lusotitan* and *Zby*) and all sauropod taxa of the Villar del Arzobispo Formation (*Turiasaurus*, *Aragosaurus*, *Losillasaurus* and *Galveosaurus*). Furthermore, two unpublished specimens from the Praia de Amoreira-Porto Novo Fm. (upper Kimmeridgian-basal Tithonian) are also incorporated. The complete dataset on which analysis has been made is composed by 95 taxa and 464 morphological characters.

The results of the phylogenetic analysis support that: *i*) *Zby atlanticus* is a turiasaur more closely related to *Turiasaurus* than *Losillasaurus*; *ii*) Turiasauria correspond to an eusauropod clade more derived than Mamenchisauridae and composed by three Iberian taxa; *iii*) *Dinheirosaurus* is a diplodocine diplodocid more derived than *Supersaurus*, *Tornieria* and *Kaatedocus*; *iv*) SHN (JJS) 177 is a diplodocine closely related to *Diplodocus* than to *Barosaurus*, supporting the presence of more than one diplodocine taxon in the Portuguese Upper Jurassic; *v*) *Lourinhasaurus alenquerensis* is a camarasaurid, sister taxa of the Morrison Formation genus, *Camarasaurus*; *vi*) Camarasauridae is a monophyletic clade including *Camarasaurus*, *Lourinhasaurus* and *Tehuelchesaurus*; *vii*) *Lusotitan atalaiensis* is a brachiosaurid titanosauriform; *viii*) Brachiosauridae is a monophyletic clade, but the relationships within the group still remain unclear; *ix*) SHN 181, is a new basal macronarian more derived than *Aragosaurus* and more primitive than *Europasaurus* + Titanosauriformes.

The Upper Jurassic sauropod faunas of the Lusitanian Basin are composed by turiasaurs, diplodocines, camarasaurids, non-titanosauriforms macronarians and brachiosaurids. Some

of these taxa (*Dinheirosaurus*, SHN (JJS) 177 and *Lourinhasaurus*) are more closely related to North-American forms than with the Gondwanan ones. This might be a consequence of a common history close in time among these territories. So far, Portuguese and Spanish Upper Jurassic sauropods are very similar faunistic assemblages, composed by taxa that are closely related in the phylogeny. Nevertheless, new discoveries are important to improve the knowledge of some group not well represented in the Villar del Arzobispo Formation, such as brachiosaurids, camarasaurids and diplodocines.

13.9. ACKNOWLEDGMENTS

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13.10. REFERENCES

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CHAPTER 14

Results

14.1. Results

14.2. Resultados

14.1. RESULTS

The results obtained herein provide important information related with the main objectives of this thesis. The present study performs the systematic evaluation of the Upper Jurassic sauropods from the Lusitanian Basin, including published and unpublished material, providing an updated phylogenetic approach for this group in the Iberian territory. The stratigraphic distribution for the major sauropod clades is provided, as well as, the evaluation of the relationships among the Portuguese faunas and the synchronous faunas of Spain, North America and Africa.

The main results discussed in the present thesis are correlated with each of the specific objectives proposed:

General hypothesis: The present phylogenetic analysis proposes a new phylogenetic approach for the Portuguese Upper Jurassic sauropods. This phylogenetic analysis includes for the first time all Upper Jurassic taxa of Portugal (*Lourinhasaurus*, *Dinheirosaurus*, *Lusotitan* and *Zby*) and Spain (*Turiasaurus*, *Aragosaurus*, *Losillasaurus* and *Galveosaurus*). Furthermore, two unpublished specimens found in sediments of the Praia de Amoreira-Porto Novo Formation (upper Kimmeridgian-basal Tithonian) are also incorporated. This phylogenetic hypothesis is based on a dataset composed by 95 taxa and 464 morphological characters.

The proposed phylogenetic hypothesis concludes: *i*) *Zby atlanticus* is a turiasaur more closely related to *Turiasaurus* than to *Losillasaurus*; *ii*) Turiasauria correspond to a basal eusauropod monophyletic clade more derived than Mamenchisauridae, being composed by three Iberian taxa; *iii*) *Dinheirosaurus* is a diplodocine diplodocid more derived than *Supersaurus*, *Tornieria* and *Kaatedocus*; *iv*) SHN (JJS) 177 is a diplodocine more closely related to *Diplodocus* than *Barosaurus*; *v*) *Lourinhasaurus alenquerensis* is a camarasaurid, constituting the sister taxon of the Morrison Formation genus *Camarasaurus*; *vi*) Camarasauridae is a monophyletic clade including *Camarasaurus*, *Lourinhasaurus* and *Tehuelchesaurus*; *vii*) *Lusotitan atalaiensis* is a brachiosaurid titanosauriform; *viii*) Brachiosauridae is a monophyletic clade, but the relationships among the members of this group still remains unclear; *ix*) SHN 181, is a new taxon more derived than *Aragosaurus* and more primitive than *Europasaurus* + Titanosauriformes.

In conclusion, the Upper Jurassic sauropod faunas of the Lusitanian Basin are composed by turiasaurs, diplodocines, camarasaurids, non-titanosauriform macronarians and brachiosaurids.

1.a. *Lourinhasaurus alenquerensis* is a valid taxon and an exclusive form of the Portuguese Upper Jurassic record, being supported by the following autapomorphies: (1) anterior-to-middle dorsal vertebrae with transversely concave ventral face bounded by longitudinal smooth crests; (2) sagittal keel in the dorsal margin of the sacral neural spines; (3) when the sacral neural spines are vertical, they becomes significantly higher posteriorly, and the dorsal margin bears a marked anterior slope; (4) prespinal process with a sagittal lamina (prespinal lamina) in the dorsal sector of the sacral spine subdividing a smooth prespinal fossa; (5) circular and deep spinoprezygapophyseal fossa on the anterior caudals (also shared by *Jobaria*); (6) the dorsal surface of the most proximal caudal neural spine slopes anteriorly transiting continuously to the anterior face of the spine, and the posterior edge produces a transverse hooked-like process in lateral view; (7) circular process on distal surface of carpal II; (8) longitudinal crest in ventral margin of ilium postacetabular process near ischiatic peduncle; (9) posterior orientation of the postacetabular process with the chord through the ischiatic and pubic articulations passing through ventral margin of the postacetabular process; (10) axis of the pubic peduncle and ischiatic articulation being parallel; (11) marked crest and groove bordering the lateral margin of acetabulum in the ischium; (12) tibia and fibula of equal length, implying a more distal position of the fibula relative to the tibia for the reception of the astragalus; and (13) marked deflection of the entire femoral shaft without lateral bulge.

The previously proposed assignation to *Lourinhasaurus alenquerensis* of some specimens from São Bernardino, Areia Branca, Porto das Barcas, Salir de Matos, Alcobaça, Praia de Santa Cruz, Chiqueda de Cima, Vale Frades, Foz do Arelho, São Mamede, Torres Vedras and Ourém is not supported here. These specimens are incomplete, representing indeterminate sauropods or eusauropods, with the exception of the Vale de Frades specimen, tentatively assigned to cf. *Duriatitan humerocristatus*.

1.b. *Lourinhasaurus alenquerensis* is recovered as a member of Camarasauridae. The present phylogenetic approach supports the monophyly of Camarasauridae, which includes *Camarasaurus*, *Lourinhasaurus* and *Tehuelchesaurus*. Camarasauridade is supported by two synapomorphies: *i*) the absence of a prespinal lamina on the dorsal vertebrae; *ii*) and the presence of a wide medial fossa on the dorsal neural spines. Camarasauridae is present in the Upper Jurassic record of North America, Europe and South America.

1.c. *Camarasaurus* and *Lourinhasaurus* constitute a monophyletic clade, supported by three synapomorphies: *i*) anterior and middle non-bifid dorsal neural spines with a transversely concave dorsal margin; *ii*) scapular blade with a rounded expansion on the acromial side; and *iii*) angle between the ischiatic peduncle and the acetabulum less than 60º.

2.a. *Lusotitan atalaiensis* is a valid taxon and an exclusive form of the Portuguese Upper Jurassic record, supported by the following autapomorphies: (1) the spinodiapophyseal lamina does not reach the distal process on the sacral neural spines; (2) small lateral projection of the spinopostzygapophyseal lamina at mid-height of the most anterior sacral spine; (3) dorsolaterally convex caudal ribs of the anteriormost caudal vertebrae in posterior view; (4) anterior-to-middle caudal postzygapophyses transversely compressed, constituting elongated processes that project well beyond the posterior margin of the neural arch; (5) presence of transverse elongated or T-shaped pits in the middle caudal vertebrae, (6) circular fossae in the ventral face of the middle caudals, anteriorly located to the chevron facets; (7) presence of bridged proximal chevrons; (8) dorsoventrally short ischiatic peduncle of the pubis; (9) pubic blade with a marked anterior orientation; (10) anterior margin of the pubis blade bearing a rounded projection; (11) pubic peduncle of the ischium constricted in anterior view; (12) tibia strongly bowed laterally; (13) no vertical groove extending up the shaft between the lateral and medial malleoli of the tibia; (14) tibial crest ventrally directed; (15) acute lateral margin of the tibia, bordered by dorsoventral smooth grooves; (16) abrupt transition between the dorsal surface of the articular surface of the ascending process and the lateral surface of the tibial shaft.

The systematic revision of the referred material to *Lusotitan atalaiensis* found in Areia Branca, Maceira, Alcobaça, Cambelas and Praia das Almoinhas does not support the previous systematic approaches, with the exception of a caudal vertebra found in Maceira, considered herein as cf. *Lusotitan atalaiensis*.

2.b. *Lusotitan* is considered a representative of Titanosauriformes. This assignation is supported by the presence of swept backwards caudal ribs on the anterior caudal vertebrae, and by dorsoventrally compressed anterior caudal vertebrae. The placement of *Lusotitan* within Brachiosauridae is supported by the presence of blind fossae on the anterior caudal vertebrae; hyposphene ridge on the anterior caudal vertebrae; and dorsoventrally compressed middle-to-posterior caudal vertebrae. The resolution within Brachiosauridae is low.

3.a *Dinheirosaurus lourinhanensis* is a diplodocine sauropod that can be diagnosed by the following autapomorphies: (1) ventral keel restricted to the posterior portion of the centrum in the posterior cervical vertebrae (unique within Flagellicaudata); (2) three small fossae on the lateral face of the neural spine in the posterior cervical vertebrae, posterior to the elongated coel; and (3) dorsal centrum length (excluding articular 'ball') being approximately the same along all the dorsal sequence (unique within Diplodocinae).

3.b. The present analysis suggests that *Dinheirosaurus* is a more derived diplodocine than *Supersaurus*, *Kaatedocus* and *Tornieria*, and a distinct form from *Supersaurus* genus. Besides the presence of four autapomorphies, *Dinheirosaurus* could be distinguished from *Supersaurus* by the presence of a shallow, anteroposteriorly elongate fossa, posteroventrally located in the lateral face of the cervical vertebrae; roughened lateral aspect of the prezygodiapophyseal lamina on the posterior cervical vertebrae; medially restricted postspinal lamina on anterior caudal vertebrae; well-developed dorsal bifurcation on the anterior caudal neural spines; and anterior caudal vertebrae with concavo-convex zygapophyseal articulation. The full preparation of the holotype will be important to provide more information about the phylogenetic context of this taxon within Diplodocinae.

4.a. Some differences are identified in *Zby atlanticus* when it is compared with other turiasaurian sauropods. The detailed comparison between *Zby* and other turiasaurs does not confirm the previously proposed diagnosis. Herein, we tentatively propose a revised diagnosis for *Zby atlanticus* based on the following exclusive features within Turiasauria: (1) ulna arched where the convexity face posteriorly (shared with *Cetiosaurus oxoniensis*); (2) presence of a crest in the lateral border of the proximal end of the radius; (3) sharp crest along the lateroventral border of the radius diaphysis; and (4) manual ungual phalanx I-2 subrectangular in lateral view.

4.b. *Zby atlanticus* is recovered as a non-neosauropod eusauropod within Turiasauria, as the sister taxa of *Turiasaurus riodevensis*. The phylogenetic position of *Zby atlanticus* within Turiasauria is supported by: *i*) the presence of dorsoventrally constricted humeral deltopectoral crest; *ii*) humeral distal condyles exposed on the distal end anterior face; *iii*) strong bulge at the level of the deltopectoral crest on the humeral posterior face and *iv*) deeply concave posterior face of the humeral distal end. *Zby atlanticus* and *Turiasaurus riodevensis* resulted in a monophyletic clade supported by only one synapomorphy: distal end of the radius beveled 20º.

5. SHN 181, a specimen found in the sediments of Praia de Amoreira-Porto Novo Formation (upper Kimmeridgian-basal Tithonian), represents a new taxon featured by: (1) sagittal longitudinal groove in the most proximal caudal neural spines; (2) apex of the most anterior caudal neural spines anteroposterioly constricted, resulting in an X in dorsal view; (3) anterior caudal vertebrae with a medial accessory articulation on the prezygapophyses, (4) lateral depression on the apex of the caudal neural spines (shared with *Aragosaurus*); (5) transverse furrow on the chevron articulations (shared by *Phuwiangosaurus* + *Tangvayosaurus*); (6) circular rough tuberosity in the medial side of the scapula; (7) elliptical concavity on the ventral face of the scapular blade base; (8) maximum diameter of the ischiatic distal end being twice than the minimum one; (9) ischium shorted than pubis (shared with titanosaurs); (10) robust fourth trochanter located in midline of the femoral posterior face (shared with *Euhelopus*, *Mamenchisaurus* and *Omeisaurus*); and (11) rectangular morphology of fibular proximal end in lateral view. Some of these features are unreported in the Upper Jurassic and shared with some Cretaceous titanosauriforms. SHN 181 is more derived than *Aragosaurus* and more primitive than *Europasaurus*, which represents the sister taxa of the Titanosauriformes.

6. The detailed study of several other specimens found along the Lusitanian Basin allows identifying several forms related to turiasaurs, diplodocines, basal macronarians (including camarasaurids) and titanosauriforms (including brachiosaurids).

The present work describes and discusses a sample of sauropod teeth, identifying four main tooth morphologies: heart-, spatulate-, compressed cone-chisel- and pencil-shaped teeth. This suggests the presence of non-neosauropod eusauropods, probably related with Turiasauria (heart-shaped teeth); basal macronarians (spatulate-shaped teeth); basal titanosauriforms (compressed cone-chisel-shaped teeth); and diplodocoids (pencil-shaped teeth).

Heart-shaped teeth are relatively abundant in the Upper Jurassic sediments of the Lusitanian Basin. An important variability is identified being defined three distinct morphotypes. This morphological variability is probably related with the different position on the tooth row.

Up to the moment, the heart-shaped teeth were only found associated with turiasaurian non-dental material. Nevertheless, the presence of this tooth morphology in the Middle Jurassic up to the Lower Cretaceous in Africa and Europe suggests a wider stratigraphic and paleogeographic range, that could reflects a wider phylogenetic distribution. The assignation of heart-shaped teeth to Turiasauria should be taken with caution.

Spatulate-shaped teeth are present along the Upper Jurassic sequence of the Lusitanian Basin. The presence of a complex cingulum (more than one lingual facet, a medial ridge and rounded bosses) suggested the placement of these teeth in Macronaria clade.

Three distinct morphotypes are defined for the compressed cone-chisel-shaped teeth. The morphological variability on the overall morphology of the crown and on the wrinkling pattern might be explained by different positions on the tooth row or by different ontogenetic stages, but new material is need in order to test this hypothesis. The present morphology is exclusive of basal titanosauriforms. The presence of an apex that twisted axially through an arc more than 45° suggests that they might belong to Brachiosauridae.

Four specimens collected in Baleal, Praia da Areia Branca, Paimogo and Praia da Corva are the first references of the presence of procoelous caudal vertebrae in the Upper Jurassic of the Lusitanian Basin. The presence of slight procoelous, fan-shaped caudal ribs with smooth prezygapophyseal centrodiapophyseal fossa is a combination that allow us to attribute the described specimens to the Eusauropoda clade. The relation of the Portuguese specimens to the Turiasauria clade is not ruled out and they share a similar morphology with the preserved anterior caudal vertebrae of *Losillasaurus*, and Puntal de Santa Cruz and San Lorenzo turiasaurs.

The sauropod fossil record of the north region of the Central Sector of the Lusitanian Basin (central and northern region of Bombarral Sub-basin) is relatively poor. The diversity found in this area (indeterminate eusauropods, including turiasaurs, diplodocines and basal titanosauriforms) is in accordance with the paleobiodiversity found in the southern part of the Bombarral Sub-basin, and in the Turcifal and Arruda Sub-basins, that includes diplodocines, camarasaurids, basal titanosauriforms and turiasaurs.

6.b. The Upper Jurassic sauropod fossil record is well represent in the sequence of the Central Sector of the Lusitanian Basin, being particularly abundant in the Bombarral and Turcifal Sub-basins. Sauropods are present along the continental deposits of the Lusitanian Basin, being recorded in the Alcobaça, Praia de Amoreira-Porto Novo, Sobral, Freixial and Bombarral Formations. Some areas of the Bombarral Sub-basin and Arruda Sub-basin still remains poorly understood due to the presence of scarce and incomplete material. No particular stratigraphic pattern was identified along the Upper Jurassic sequence, and the major clades are present along all the lower Kimmeridgian to the upper Tithonian continental deposits.

7. The Upper Jurassic-Lower Cretaceous sauropod record of Spain shares the presence of diplodocines and non-titanosauriform basal macronarians with the sauropod faunas of the Upper Jurassic of the Lusitanian Basin (brachiosaurid or camarasaurid was not identified in the Spanish territory). *Galveosaurus herreroi* might represent a junior synonymous of *Lusotitan atalaiensis*. *Turiasaurus*, *Losillasaurus* and *Aragosaurus* are taxa closely related to the Portuguese Upper Jurassic forms.

8. The supposed close relationship of the Portuguese sauropods with taxa from the North American Upper Jurassic of the Morrison Formation is less close than that interpreted from other faunistic groups, such as theropod dinosaurs. Diplodocines and camarasaurids described for the Upper Jurassic of Portugal are more closely related to the Morrison forms than to the Gondwanan representatives. The closer relationship among Portuguese and North-American forms can be explained by and a more recent common history of these territories. The phylogenetic affinities of the Portuguese Upper Jurassic brachiosaurids remain unclear, resulting from a low resolution

within the Brachiosauridae clade. Turiasauria is recognized as a diverse non-neosauropod eusauropod group in the Iberian territory when compared with diplodocids, camarasaurids and brachiosaurids, being represented by three taxa, *Turiasaurus*, *Losillasaurus* and *Zby*.

14.2. RESULTADOS

Los resultados obtenidos en los diferentes trabajos efectuados durante esta tesis aportan información relevante relacionada con los objetivos propuestos. Esta tesis resulta en la revisión sistemática del registro de saurópodos del Jurásico Superior de la cuenca lusitánica, incluyendo material publicado e inédito. Se presenta también una propuesta filogenética actualizada para este grupo de dinosaurios en el territorio ibérico. Se discute la distribución estratigráfica para los grupos representados, así como las relaciones de parentesco con las formas sincrónicas de España, Norteamérica y África.

Los resultados principales relacionados con cada una de las hipótesis y objetivos propuestos en el capítulo 2 son:

Hipótesis general: El estudio realizado propone una nueva hipótesis filogenética para los saurópodos del Jurásico Superior portugués. El presente análisis filogenético incorpora por primera vez todos los taxones portugueses (*Lourinhasaurus*, *Dinheirosaurus*, *Lusotitan* and *Zby*) y españoles (*Turiasaurus*, *Aragosaurus*, *Losillasaurus* and *Galveosaurus*). Además, dos especímenes inéditos recolectados en los sedimentos de la Formación Praia de Amoreira-Porto Novo (Kimmeridgiense superior-Titoniense basal) fueron también introducidos en el análisis. La hipótesis filogenética propuesta está basada en una matriz compuesta por 95 taxones y 464 caracteres morfológicos.

La hipótesis filogenética propuesta permite concluir que: *i*) *Zby atlanticus* es un turiasaurio más estrechamente emparentado con *Turiasaurus* que con *Losillasaurus*; *ii*) Turiasauria es un clado monofilético más derivado que Mamenchisauridae, compuesto por tres taxones ibéricos; *iii*) *Dinheirosaurus* es un diplodocino más derivado que *Supersaurus*, *Tornieria* y *Kaatedocus*; *iv*) SHN (JJS) 177 es un diplodocino más estrechamente relacionado con *Diplodocus* que con *Barosaurus*, *v*) *Lourinhasaurus alenquerensis* es un camarasáurido, que constituye el taxón hermano del género de la Formación Morrison *Camarasaurus*; *vi*) Camarasauridae es un grupo monofilético que incluye *Camarasaurus*, *Lourinhasaurus* y *Tehuelchesaurus*; *vii*) *Lusotitan atalaiensis* es un titanosauriforme braquiosáurido; *viii*) Brachiosauridae es un clado monofilético, pero las relaciones de parentesco entre los taxones que lo componen no ofrecen una alta resolución; *ix*) SHN 181 es un nuevo macronario basal, más derivado que *Aragosaurus* y más primitivo que *Europasaurus* + Titanosauriformes.

Considerando todas estas ideas, las faunas del Jurásico Superior de la cuenca lusitánica están compuestas por turiasaurios, diplodocinos, y macronarios basales, incluyendo camarasáuridos y braquiosáuridos.

1.a. *Lourinhasaurus alenquerensis* es un taxón valido, exclusivo del Jurásico Superior portugués, definido mediante las siguientes autapomorfías: (1) vértebras dorsales anteriores y medias con la cara ventral transversalmente cóncava y limitada por crestas ventrolaterales; (2) quilla sagital en el margen dorsal de las espinas sacras; (3) cuando las espinas sacras están verticalizadas, su altura aumenta progresivamente hacia la región posterior; (4) proceso prespinal con una lámina sagital (lámina prespinal) en el sector dorsal de la espina sacra que produce la subdivisión de la incipiente fosa prespinal; (5) fosa espinoprezigapofiseal circular y profunda en las vértebras caudales anteriores (carácter compartido con *Jobaria*); (6) superficie dorsal de la espina caudal más proximal inclinándose anteriormente y extendiéndose de forma continua hacia su cara anterior, y borde posterior de esta superficie dorsal presentando un perfil con forma de gancho en vista lateral;

(7) proceso circular en la superficie distal del carpiano II; (8) cresta longitudinal en el borde ventral del proceso postacetabular del ilion y cercana al pedúnculo isquiático; (9) proceso postacetabular orientado posteriormente cuando las superficies de articulación con el pubis y el isquion están en el plano horizontal; (10) ejes del pedúnculo púbico e isquiático paralelos; (11) cresta pronunciada y surco asociado en el margen lateral del acetábulo; (12) tibia y fíbula con igual longitud, resultando en una posición más distal para la fíbula en relación a la tibia para la recepción del astrágalo; y (13) desviación pronunciada de la diáfisis del fémur sin la presencia de comba lateral.

La propuesta sistemática que consideraba la atribución de algunos especímenes clásicos provenientes de las localidades de São Bernardino, Areia Branca, Porto das Barcas, Salir de Matos, Alcobaça, Praia de Santa Cruz, Chiqueda de Cima, Vale Frades, Foz do Arelho, São Mamede, Torres Vedras y Ourém al taxón *Lourinhasaurus alenquerensis* es refutada. La mayoría de estos especímenes son incompletos y representan formas indeterminadas de saurópodos y eusaurópodos, excepto un espécimen de Vale de Frades atribuido a cf. *Duriatitan humerocristatus*.

1.b. *Lourinhasaurus alenquerensis* es un miembro del clado Camarasauridae. Este clado es monofilético, estando compuesto por *Camarasaurus*, *Lourinhasaurus* y *Tehuelchesaurus*. Camarasauridae es soportado por dos sinapomorfías: la ausencia de lámina prespinal en las vértebras dorsales y la presencia de una fosa medial amplia en las espinas dorsales. Este clado está presente en el Jurásico Superior de Europa y Norteamérica y Sudamérica.

1.c. *Camarasaurus* y *Lourinhasaurus* corresponden a un grupo monofilético, soportado por tres sinapormorfías: espinas dorsales anteriores y medias no bifurcadas, con margen dorsal transversalmente cóncavo; lámina escapular con expansión redondeada en su margen acromial; ángulo entre el pedúnculo isquiático y el acetábulo inferior a 60º.

2.a. *Lusotitan atalaiensis* es un taxón válido, exclusivo del Jurásico Superior portugués, caracterizado por las siguientes autapomorfías: (1) la lámina espinodiapofiseal no alcanza el proceso distal de las espinas sacras; (2) proyección lateral de la lámina espinopostzigapofiseal a media altura en las espinas sacras anteriores; (3) vértebras caudales más proximales con costillas caudales de margen dorsolateral convexo en vista posterior; (4) vértebras caudales anteriores y medias con postzigapófisis transversalmente comprimidas, constituyendo un proceso alargado y posteriormente proyectado respecto al margen posterior del arco neural; (5) presencia de surcos transversalmente alargados o en forma de T en las vértebras caudales medias; (6) fosas circulares en la cara ventral de los centros de las vértebras caudales medias, localizadas anteriormente a las articulaciones posteriores para los chevrones; (7) presencia de chevrones anteriores con margen dorsal cerrado; (8) pedúnculo isquiático del pubis dorsoventralmente corto; (9) lámina púbica orientada anteriormente; (10) margen anterior de la lámina púbica con proyección redondeada; (11) pedúnculo púbico del isquion comprimido a la mitad de su altura en vista anterior; (12) tibia fuertemente arqueada en vista anterior; (13) surco vertical en la cara posterior del extremo distal de la tibia entre los maléolos lateral y medial; (14) cresta cnemial ventralmente dirigida; (15) margen lateral de la diáfisis de la tibia agudo, y bordeado por suaves surcos proximodistales; (16) transición abrupta entre la superficie dorsal de la articulación del proceso ascendente y la cara lateral de la diáfisis de la tibia.

La propuesta sistemática que consideraba la atribución de algunos especímenes clásicos provenientes de las localidades de Areia Branca, Maceira, Alcobaça, Cambelas y Praia das Almoinhas al taxón *Lusotitan atalaiensis* es refutada. La mayoría de estos especímenes son incompletos y representan formas indeterminadas de saurópodos y eusaurópodos, excepto un espécimen encontrado en la localidad de Maceira que es atribuido a cf. *Lusotitan atalaiensis*.

2.b. *Lusotitan* es considerado un miembro del clado Titanosauriformes. Esta relación sistemática es soportada por la presencia de costillas caudales orientadas posteriormente y vértebras caudales anteriores dorsoventralmente comprimidas. El posicionamiento de *Lusotitan* en el

clado Brachiosauridae es soportado por la presencia de *i*) fosas poco profundas en las vértebras caudales anteriores; *ii*) cresta hiposfénica en las vértebras caudales anteriores; y *iii*) vértebras caudales medias y posteriores dorsoventralmente comprimidas. La resolución dentro del clado Brachiosauridae es baja.

3.a *Dinheirosaurus lourinhanensis* es un diplodocino caracterizado por las siguientes autapomorfías: (1) vértebras cervicales posteriores con cresta ventral en la porción posterior de los centros vertebrales (exclusivo en Flagellicaudata); (2) tres pequeñas fosas en la cara lateral de la espina neural de las vértebras cervicales posteriores, localizadas posteriormente a la fosa alargada; y (3) longitud del centro dorsal (excluyendo el cóndilo) constante a lo largo de la serie axial (exclusivo en Diplodocinae).

3.b. El análisis filogenético propuesto sugiere que *Dinheirosaurus* es un diplodocino más derivado que *Supersaurus*, *Kaatedocus* y *Tornieria*. También se concluye que es una forma distinta de *Supersaurus*. Además de la presencia de cuatro autapomorfías, *Dinheirosaurus* se diferencia de *Supersaurus* por la presencia de una fosa anteroposteriormente alargada localizada en el extremo posteroventral del centro vertebral de las vértebras cervicales; aspecto lateral rugoso de la lámina prezigadiapofiseal en las vértebras cervicales posteriores; lámina postespinal medialmente restringida en las vértebras caudales anteriores; desarrollo de bifurcación dorsal de las espinas caudales anteriores; y caudales anteriores con articulación zigapofiseal cóncavo-convexa. La finalización de la preparación del holotipo podrá añadir información importante para ayudar a establecer las relaciones de parentesco con otros diplodocinos.

4.a. *Zby atlanticus* muestra algunas diferencias al ser comparado con otros turiasaurios. La comparación detallada entre *Zby* y otros turiasaurios permite revisar la diagnosis propuesta anteriormente. *Zby atlanticus* se caracteriza por las siguientes autapomorfias: (1) ulna arqueada con la convexidad dirigida posteriormente (carácter compartido con *Cetiosaurus oxoniensis*); (2) cresta en el borde lateral de la extremidad proximal del radio; (3) cresta afilada presente a lo largo del borde lateroventral de la diáfisis del radio; y (4) falange ungueal I-2 de la mano subrectangular en vista lateral.

4.b. *Zby atlanticus* se considera un eusaurópodo basal dentro del clado Turiasauria, identificándose como el taxón hermano de *Turiasaurus riodevensis*. La posición filogenética dentro del clado Turiasauria es soportada por la presencia de: *i*) cresta deltopectoral dorsoventralmente restringida, *ii*) tuberosidad en la cara posterior del húmero, por detrás de la cresta deltopectoral, y *iii*) cara posterior de la sección distal del húmero marcadamente cóncava. *Zby* y *Turiasaurus* forman un grupo monofilético soportado por una única sinapomorfia: cara distal del radio inclinada cerca de 20º respecto al plano horizontal.

5. El ejemplar SHN 181, proveniente de los sedimentos de la Formación Praia de Amoreira-Porto Novo (Kimmeridgiense superior-Titoniense basal), representa un nuevo taxón caracterizado por: (1) surco longitudinal y sagital en la cara dorsal de las espinas caudales más proximales; (2) ápice de las espinas caudales anteriores anteroposteriormente constreñido, resultando en un contorno en X en vista dorsal; (4) depresión lateral en el ápice de las espinas caudales anteriores (carácter compartido con *Aragosaurus*); (5) surco transversal en las articulaciones de los chevrones (carácter compartido con *Phuwiangosaurus* + *Tangvayosaurus*); (6) tuberosidad circular y rugosa en la cara medial del sector más posterior del proceso acromial; (7) concavidad elíptica en la cara ventral de la base de la lámina escapular; (8) diámetro máximo de la sección distal del isquion dos veces el diámetro mínimo; (9) isquion más corto que el pubis (carácter compartido con los titanosaurios); (10) cuarto trocánter colocado en medio de la cara posterior de la diáfisis del fémur (carácter compartido por *Euhelopus*, *Mamenchisaurus* y *Omeisaurus*); y (11) morfología rectangular de la extremidad proximal de la fíbula en vista lateral. Algunos de estos caracteres no han sido registrados en el Jurásico Superior y están compartidos con algunos Titanosauriformes del Cretácico Superior. SHN 181 es una forma más derivada que *Aragosaurus* y más primitiva que *Europasaurus*, grupo hermano de los Titanosauriformes.

6.a. El estudio detallado de muchos otros especímenes encontrados en la cuenca lusitánica ha permitido identificar varias formas relacionadas con los turiasaurios, diplodocinos, macronarios basales (incluyendo los camarasáuridos) y los Titanosauriformes (incluyendo los braquiosáuridos).

El presente trabajo describe y discute una muestra de numerosos dientes de saurópodo, identificando cuatro morfotipos distintos: en forma de corazón, espátula, lápiz y cono-cincel comprimido. La identificación de estos morfotipos en el Jurásico Superior portugués sugiere la presencia de eusaurópodos basales probablemente relacionados con Turiasauria, macronarios basales, titanosauriformes y diplodocoides.

Los dientes en forma de corazón son relativamente abundantes en el Jurásico Superior de la cuenca lusitánica. La alta variabilidad morfológica identificada resulta en la definición de tres morfotipos. Esta variabilidad puede deberse a la posición del diente en la serie dentaria. De momento, los dientes ibéricos en forma de corazón han sido únicamente encontrados en asociación con material no dentario de saurópodos turiasaurios. Sin embargo, este tipo de morfología se encuentra registrada desde el Jurásico Medio al Cretácico Inferior en África y Europa, apuntando hacia un mayor rango estratigráfico y paleogeográfico. Esto puede reflejar también una mayor distribución filogenética. Por tanto, la asignación de estos dientes al clado Turiasauria debe ser considerada con precaución.

Los dientes en forma de espátula están presentes a lo largo de toda la secuencia del Jurásico Superior de la cuenca lusitánica. La presencia de cíngulo complejo (más de una faceta lingual, cresta medial y una tuberosidad redondeada) sugiere que estos dientes podrían pertenecer a saurópodos macronarios.

Los dientes en forma de cono-cincel comprimido presentan una importante variabilidad morfológica. Se han establecido tres morfotipos distintos. La variabilidad descrita puede tener origen tanto posicional como ontogenético. Sin embargo, es necesario nuevo material para testar esta hipótesis. Esta morfología es exclusiva de los Titanosauriformes y la presencia de una rotación de más de 45º del ápice sugiere que podrían pertenecer a miembros del clado Brachiosauridae.

Cuatro vértebras caudales de las localidades de Baleal, Praia da Areia Branca, Paimogo y Praia da Corva suponen las primeras referencias a vértebras procélicas de saurópodos del Jurásico Superior de la cuenca lusitánica. La presencia de una condición procélica poco desarrollada y costillas caudales en forma de abanico, con una fosa prezigapofiseal centrodiapofiseal somera, es una combinación de caracteres que permite relacionar estos especímenes con eusaurópodos basales. La atribución de estas vértebras a Turiasauria no puede ser excluida. La morfología de estos ejemplares es similar a la presentada por *Losillasaurus* y los turiasaurios de Puntal de Santa Cruz y San Lorenzo.

La región norte y central de la sub-cuenca de Bombarral presenta un escaso registro fósil en saurópodos. El estudio sistemático de los saurópodos de esta área permite identificar la presencia de eusaurópodos indeterminados, turiasaurios, diplodocinos y titanosauriformes. Esta composición faunística es coherente con la paleodiversidad conocida tanto en el sur de la sub-cuenca de Bombarral, como en las sub-cuencas de Turcifal y Arruda, constituida por turiasaurios, diplodocinos y macronarios (incluyendo camarasáuridos y braquiosáuridos).

6.b. El registro fósil de saurópodos está bien representado en la secuencia sedimentaria del Jurásico Superior de la cuenca lusitánica, y es particularmente abundante en la sub-cuencas de Bombarral y Turcifal. Los saurópodos se encuentran registrados a lo largo de los depósitos continentales de las Formaciones Alcobaça, Praia de Amoreira-Porto Novo, Sobral, Freixial y Bombarral. Algunas áreas de las sub-cuencas de Bombarral y Arruda apenas han sido prospectadas. Por tanto, su registro es poco conocido, correspondiendo a material escaso y fragmentario. Ningún patrón estratigráfico ha sido identificado a lo largo de la secuencia sedimentaria estudiada, con los principales clados de saurópodos presentes a lo largo de los niveles datados entre el Kimmeridgiense inferior y el Titoniense superior.

7. Las faunas de saurópodos del Jurásico Superior-Cretácico basal de España están compuestas por turiasaurios, diplodocinos y macronarios basales, una composición faunística similar a la del Jurásico Superior de la cuenca lusitánica, excepto por la ausencia de camarasáuridos y braquiosáuridos. El taxón español *Galveosaurus herreroi* podría corresponder a un sinónimo de la forma portuguesa *Lusotitan atalaiensis*. *Turiasaurus*, *Losillasaurus* y *Zby atlanticus* están estrechamente emparentados y son miembros del clado Turiasauria.

8. Las relaciones de parentesco entre los saurópodos del Jurásico Superior portugués y las formas del Jurásico Superior de la Formación Morrison (EEUU) son menos estrechas que aquellas reconocidas para otros grupos faunísticos, como por ejemplo en los dinosaurios terópodos. Sin embargo, los diplodocinos y los camarasáuridos descritos en la cuenca lusitánica están más cercanamente emparentados con los saurópodos de la Formación Morrison que con los representantes gondwánicos. Esto puede ser explicado como resultado de un contacto faunístico más reciente entre estos dos territorios. Las afinidades filogenéticas de los braquiosáuridos del Jurásico Superior portugués permanecen sin clarificar debido a la baja resolución presentada por el clado Brachiosauridae en la hipótesis propuesta. En el territorio ibérico, los turiasaurios son un grupo diverso de eusaurópodos basales, con tres taxones descritos: *Turiasaurus*, *Losillasaurus* y *Zby*.

CHAPTER 15

Conclusions

15.1. Conclusions

15.2. Conclusiones

15.1. CONCLUSIONS

The systematic study of the sauropod fossil record of the Upper Jurassic of the Lusitanian Basin is performed here, based on a new phylogenetic analysis. It includes, for the first time, all Upper Jurassic-basal Cretaceous sauropod taxa from both Portugal (*Lourinhasaurus*, *Dinheirosaurus*, *Zby* and *Lusotitan*) and Spain (*Turiasaurus*, *Aragosaurus*, *Losillasaurus* and *Galveosaurus*). This phylogenetic hypothesis is based on a dataset composed by 95 taxa and 464 morphological characters.

The sauropod fossil record is well-represent on the Upper Jurassic sequence of the Central Sector of the Lusitanian Basin, being particular abundant in the Bombarral and Turcifal Sub-basins. Sauropods are reported along the continental deposits of the Alcobaça, Praia de Amoreira-Porto Novo, Sobral, Freixial and Bombarral Formations. The detailed study of several published and unpublished specimens found throughout the Upper Jurassic sedimentary sequence of the Lusitanian Basin allows identifying several forms corresponding to turiasaurs, diplodocines, basal macronarians (including camarasaurids) and titanosauriforms (including brachiosaurids). No particular stratigraphic pattern was identified along the Upper Jurassic sequence, and these major clades are present from the lower Kimmeridgian to the upper Tithonian levels.

The Upper Jurassic Portuguese sauropod faunas are recognized as composed by four valid and exclusive taxa: *Lourinhasaurus alenquerensis*, *Dinheirosaurus lourinhanensis*, *Lusotitan atalaiensis*, and *Zby atlanticus*, plus a new basal macronarian taxon and cf. *Duriatitan humerocristatus*. The diagnoses of the previously defined taxa are revised, and several exclusive characters are proposed for the new one. *Lourinhasaurus alenquerensis* is considered as a member of Camarasauridae. In spite of the morphological similarities between the *Camarasaurus* species and *Lourinhasaurus alenquerensis*, the Portuguese taxon is considered as distinct from the *Camarasaurus* species on the basis of several anatomical features, including a few exclusive ones. *Lusotitan atalaiensis* is a member of Brachiosauridae. *Dinheirosaurus* is a more derived diplodocine than *Supersaurus*, *Kaatedocus* and *Tornieria*, being a form outside the *Supersaurus* genus. *Zby atlanticus* is recovered as a non-neosauropod eusauropod within Turiasauria, as the sister taxa of *Turiasaurus riodevensis*. The so far unpublished SHN 181, found in the sediments of the Praia de Amoreira-Porto Novo Formation (upper Kimmeridgian-basal Tithonian) of Valmitão (Lourinhã), represents a new sauropod. SHN 181 is considered as a basal macronarian non-camarasaurid with several derived conditions that might indicate a process of convergence with Cretaceous derived titanosauriforms or a more derived position within Macronaria.

The Upper Jurassic-Lower Cretaceous sauropod record of Spain shares with the sauropod faunas of the Upper Jurassic of the Lusitanian Basin the presence of diplodocines and non-titanosauriform basal macronarians. Brachiosaurids and camarasaurids have been not so far identified in the Spanish territory. The supposed close relationship of the Portuguese sauropods with taxa from the North American Upper Jurassic Morrison Formation is less close than that interpreted from other faunistic groups. Diplodocine and camarasaurid forms described for the Upper Jurassic of Portugal are more closely related to the Morrison Fm. forms than to the Gondwanan representatives. The closer relationship among Portuguese and North-American forms can be explained by and a more recent common history of these territories. On the other hand, Turiasauria is probably so far restricted to the European territory during the Upper Jurassic.

5.2. CONCLUSIONES

El estudio sistemático propuesto de los saurópodos del Jurásico Superior de la Cuenca Lusitánica está basado en un nuevo análisis filogenético que incluye, por primera vez, todos los taxones del Jurásico Superior portugués (*Lourinhasaurus*, *Dinheirosaurus*, *Zby* and *Lusotitan*) y del Jurásico Superior-Cretácico basal español (*Turiasaurus*, *Aragosaurus*, *Losillasaurus* y *Galveosaurus*). Esta hipótesis filogenética fue obtenida mediante el empleo de una matriz compuesta por 95 taxones y 464 datos morfológicos.

Los saurópodos son un grupo fósil relativamente abundante en la secuencia sedimentaria del Jurásico Superior de la Cuenca Lusitánica y, en particular, en las Sub-cuencas de Bombarral y Turcifal. Este grupo está presente a lo largo de los depósitos continentales de las Formaciones Alcobaça, Praia de Amoreira-Porto Novo, Sobral, Freixial y Bombarral. El estudio sistemático del material publicado e inédito asignable a Sauropoda permite identificar la presencia de varias formas correspondientes a turiasaurios, diplodocinos, macronarios basales (incluyendo camarasáuridos) y titanosauriformes (incluyendo braquiosáuridos). La distribución estratigráfica de los grupos de saurópodos representados es homogénea a lo largo de la secuencia sedimentaria.

Las faunas de saurópodos del Jurásico Superior portugués están compuestas por cinco taxones exclusivos: *Lourinhasaurus alenquerensis*, *Dinheirosaurus lourinhanensis*, *Lusotitan atalaiensis*, *Zby atlanticus* y un nuevo taxón de Macronaria. La diagnosis de los cuatro taxones previamente definidos han sido revisadas y se han propuesto varios caracteres exclusivos para el nuevo taxón. *Lourinhasaurus alenquerensis* es considerado un miembro de Camarasauridae. Aunque *Lourinhasaurus alenquerensis* muestra numerosos caracteres morfológicos compartidos con las especies del género norteamericano *Camarasaurus*, la presencia de varios caracteres exclusivos en *Lourinhasaurus alenquerensis*, permite considerar la especie portuguesa como distinta. *Lusotitan atalaiensis* es reconocido como un miembro de Brachiosauridae. *Dinheirosaurus* se identifica como un diplodocino más derivado que *Supersaurus*, *Kaatedocus* y *Tornieria*, pero no atribuible al género *Supersaurus*. *Zby atlanticus* es considerado un eusaurópodo basal, siendo un miembro de Turiasauria reconocido como el taxón hermano de *Turiasaurus*. El ejemplar hasta ahora inédito SHN 181, encontrado en Valmitão (Formación de Praia de Amoreira-Porto Novo), representa un nuevo saurópodo. SHN 181 es un macronario basal no perteneciente a Camarasauridae que muestra con varias características compartidas con algunos titanosauriformes derivados.

Las faunas de saurópodos del Jurásico Superior-Cretácico basal de España están compuestas por turiasaurios, diplodocinos y macronarios basales, una composición faunística similar a la del Jurásico Superior de la Cuenca Lusitánica excepto por la ausencia de camarasáuridos y braquiosáuridos. Las relaciones de parentesco entre los saurópodos del Jurásico Superior portugués y las formas del Jurásico Superior de la Formación Morrison (EEUU) son menos estrechas que aquellas reconocidas para otros grupos faunísticos, como por ejemplo dinosaurios terópodos. Sin embargo, los diplodocinos y los camarasáuridos descritos en la Cuenca Lusitánica están más cercanamente emparentados con los saurópodos de la Formación Morrison que con los representantes gondwanicos, lo cual puede ser interpretado como resultado de un contacto faunístico más reciente entre estos dos territorios. En el territorio ibérico, los turiasaurios son un grupo diverso de eusaurópodos basales, con tres taxones descritos: *Turiasaurus*, *Losillasaurus* y *Zby*.

CHAPTER 16

Acknowledgments

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16.2. Agradecimentos

16.3. Agradecimientos

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Un “obrigado” eterno a Fórnea.

SUPPLEMENTARY MATERIAL

SUPPLEMENTARY MATERIAL 1

List of the sauropod material from the Upper Jurassic of the Lusitanian Basin

Number	Taxonomy		Locality	Municipality	Horizon	Anatomy
?	?	?	Vale de Frades	Lourinhã	Bombarral Fm.	Femur
GeoFCUL(AB)	?Eusauropoda	?Eusauropoda indet.	Praia da Areia Branca	Lourinhã	Bombarral Fm.	Nine middle caudal vertebrae and chevrons
MG 125	Titanosauriformes	Titanosauriformes indet.	Ourém	Ourém	Alcobaça Fm.?	Tooth
MG 277	?Turiasauria	?Turiasauria indet.	Fervença	Alcobaça	Alcobaça Fm.?	
MG 16	?Turiasauria	?Turiasauria indet.	Ourém	Ourém	Alcobaça Fm.?	Tooth
MG 25197.1-6	Diplodocinae	Diplodocinae indet.	Porto Novo	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Caudal, ribs and an indeterminate fragment
MG 25254.2-4	Sauropoda	Sauropoda indet.	Between Foz Velha da Maceira and Cambelas	Torres Vedras	Freixial Fm.	Partial caudal vertebra and indeterminate fragments
MG 27891	Titanosauriformes	Titanosauriformes indet.	Guimarota	Leiria	Alcobaça Fm.	Tooth
MG 27892	Titanosauriformes	Titanosauriformes indet.	Guimarota	Leiria	Alcobaça Fm.	Tooth
MG 27894	Titanosauriformes	Titanosauriformes indet.	Guimarota	Leiria	Alcobaça Fm.	Tooth
MG 27895	Titanosauriformes	Titanosauriformes indet.	Guimarota	Leiria	Alcobaça Fm.	Tooth
MG 30389	Sauropoda, Diplodocidae	Sauropoda indet. and Diplodocinae indet.	Batalha	Batalha	Alcobaça or Bombarral Fm.	Axial and appendicular elements
MG 30390	Eusauropoda	Sauropoda indet.	Porto das Barcas	Lourinhã	Sobral Fm.	Four anterior and middle caudal vertebrae plus indeterminate fragments
MG 30480	Sauropoda	Sauropoda indet.	Outeiro do Seixo, Ribamar	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Dorsal rib fragments
MG 30481	Neosauropoda	Neosauropoda indet.	Atalaia?	Lourinhã?	Sobral Fm.?	Partial dorsal centrum
MG 30482	Sauropoda	Sauropoda indet.	Atalaia?	Lourinhã?	Sobral Fm.?	Caudal neural spine
MG 30483	Eusauropoda	Eusauropoda indet.	?	?	?	Anterior caudal vertebra
MG 30484	Sauropoda	Sauropoda indet.	?	Alenquer?	?	Humeral distal end
MG 30485	Titanosauriformes	Titanosauriformes indet.	Moinho do Carmo?	Alenquer?	Sobral Fm.?	Pubic peduncle of an ilium
MG 30486	Turiasauria	Turiasauria indet.	Atouguia da Baleia?	Lourinhã?	Praia de Amoreira-Porto Novo Fm.?	Right fibula
MG 3783	?Macronaria	?Macronaria indet.	Baleal	Peniche	Praia de Amoreira-Porto Novo Fm.	Tooth
MG 3794, 4798, 4801, 4805-10, 4838, 4944, 4950, 4952, 4958, 4964, 4965, 4966, 4981, 4982, 4803, 4985-1, 4985 2-20, 5795, 8793, 8794, 8807 and unlabeled sacral neural spine and chevron	Brachiosauridae	*Lusotitan atalaiensis*	Peralta	Lourinhã	Sobral Fm.	Partial skeleton
MG 4799	Neosauropoda	Neosauropoda indet.	Castanheira	Vila Franca de Xira	Abadia Fm.	Middle/posterior dorsal vertebra
MG 4800	Sauropoda	Sauropoda indet.	Porto Novo	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Anterior caudal vertebra
MG 4802	Sauropoda	Sauropoda indet.	Alto da Vela, Santa Cruz	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Middle caudal vertebra
MG 4804	Eusauropoda	Eusauropoda indet.	Casal de Lã, Salir de Matos	Caldas da Rainha	Bombarral Fm.	Middle caudal vertebra
MG 4811	Sauropoda	Sauropoda indet.	Albergaria dos Doze	Pombal	Bombarral Fm.	Middle/posterior caudal vertebra
MG 4819, 4821, 4826	Diplodocinae	Diplodocinae indet.	São Gregório da Fanadia	Caldas da Rainha	Bombarral Fm.	Three partial middle/posterior caudal vertebra
MG 4832	?Turiasauria	?Turiasauria indet.	São Martinho do Porto	Caldas da Rainha	Alcobaça Fm.	Tooth
MG 4915, 4916, 4917, 4919	Diplodocidae	Diplodocidae indet	Pedras Muitas	Peniche	Bombarral Fm.	Cervical vertebrae remains
MG 4920	Eusauropoda	Eusauropoda indet.	Monte da Cruz do Facho, Foz do Arelho	Caldas da Rainha	Bombarral Fm.	Cervical or dorsal neural spine
MG 4956, 30373, 30377, 30379, 4956, 30378, 30384, 30370, 4956, 30380, 30376, 4956, 30374, 30388, 30387, 5780, 30371, 5780, 30372, 30383, 30382, 2, 30381, 4979, 4979, 30385, 5781, 4975, 4970, 4957, 4931, 4983, 4984, 30375, 30386 and unlabelled fragmentary elements	Camarasauridae	*Lourinhasaurus alenquerensis*	Moinho do Carmo	Alenquer	Sobral Fm.	Partial skeleton

Table S.1. List of the sauropod material from the Upper Jurassic of the Lusitanian Basin

Number	Taxonomy		Locality	Municipality	Horizon	Anatomy
MG 4974	Sauropoda	Sauropoda indet.	Abadia (northern of Batalha)	Leiria	Alcobaça Fm.	series
MG 4976	Eusauropoda	cf. *Duriatitan humerocristatus*	Praia dos Frades	Peniche	Praia de Amoreira-Porto Novo Fm.	Right humerus
MG 4978	Eusauropoda	Eusauropoda indet.	São Bernardino	Peniche	Praia de Amoreira-Porto Novo Fm.	16 anterior to middle caudal vertebrae
MG 4986	Titanosauriformes	Titanosauriformes indet.	Praia da Areia Branca	Lourinhã	Bombarral Fm.	Left femur
MG 8771	Sauropoda	Sauropoda indet.	Porto das Barcas	Lourinhã	Sobral Fm.	Two teeth fragments associated with "*Omasaurus lenieri* " material
MG 8772	Titanosauriformes	Titanosauriformes indet.	Praia da Areia Branca	Lourinhã	Bombarral Fm.	Tooth fragment
MG 8772	Titanosauriformes	Titanosauriformes indet.	Praia da Areia Branca	Lourinhã	Bombarral Fm.	Tooth
MG 8772	Titanosauriformes	Titanosauriformes indet.	Praia da Areia Branca	Lourinhã	Bombarral Fm.	Tooth
MG 8779	Titanosauriformes	Titanosauriformes indet.	Ourém	Vila Nova de Ourém	Alcobaça Fm.?	Tooth
MG 8783	Eusauropoda	Eusauropoda indet.	Baleal	Peniche	Praia de Amoreira-Porto Novo Fm.	Tooth
MG 8792	Sauropoda	Sauropoda indet.	Atalaia	Lourinhã	Sobral Fm.	Two dorsal rib fragments
MG 8799	Sauropoda	Sauropoda indet.	Praia das Almoinhas?	Torres Vedras?	?	Posterior caudal vertebra
MG 8800	Eusauropoda	Eusauropoda indet.	Porto das Barcas	Lourinhã	Sobral Fm.	Middle caudal vertebra
MG 8802	Sauropoda	Sauropoda indet.	?	?	?	Middle caudal vertebra
MG 8803	Sauropoda	Sauropoda indet.	Serra da Vila	Torres Vedras	Sobral Fm.	Partial tibial distal end
MG 8804	Titanosauriformes	cf. *Lusotitan atalaiensis*	Maceira	Torres Vedras	Freixial Fm.	Middle caudal vertebra
MG 8805	Sauropoda	Sauropoda indet.	Porto das Barcas	Lourinhã	Sobral Fm.	Middle caudal vertebra
MG 8809	Sauropoda	Sauropoda indet.	Atalaia	Lourinhã	Sobral Fm.	Three neural arch fragments
ML351	Eusauropoda	Eusauropoda indet.	Porto das Barcas	Lourinhã	Sobral Fm.	Partial skeleton
ML368	Turiasauria	*Zby atlanticus*	Vale de Pombas	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Partial skeleton
ML414	Diplodocinae	*Dinheirosaurus lourinhanensis*	Porto Dinheiro	Lourinhã	Fm./Sobral Fm.	Partial skeleton
ML418	Diplodocidae	Diplodocidae indet	Moita dos Ferreiros	Lourinhã	Bombarral Fm.	Cervical and dorsal vertebrae
ML684	Sauropoda	Sauropoda indet.	Lage Fria	Lourinhã	Sobral Fm.	Sternal plate
MMPM.P/307	Sauropoda	Sauropoda indet.	Golfeiros	Batalha	Alcobaça Fm.	Femoral proximal end
MMPM.P/551	Eusauropoda	Eusauropoda indet.	São Martinho do Porto	Alcobaça	Alcobaça Fm.	end
MMPM.P/554	Sauropoda	Sauropoda indet.	Fonte do Oleiro	Porto de Mós	Alcobaça Fm.	Posterior caudal vertebra
MMPM.P/587	Sauropoda	Sauropoda indet.	Albergaria	Porto de Mós	Bombarral or Alcobaça Fm.	Posterior caudal vertebra
MMPM.P/587	Sauropoda	Sauropoda indet.	São Martinho do Porto	Alcobaça	Alcobaça Fm.	Appendicular bone
MMPM.P/72	Sauropoda	Sauropoda indet.	Malásia	Caldas da Rainha	Bombarral Fm.	Appendicular bone
MMPM.P/73	Eusauropoda	Eusauropoda indet.	Paimogo	Lourinhã	Bombarral Fm. or Sobral Fm.	Anterior caudal vertebra
MMPM.P/75	Eusauropoda	Eusauropoda indet.	Imaginário	Caldas da Rainha	Bombarral Fm.	Left astragalus
MNHNUL/AND.302	Diplodocoidea	Diplodocoidea indet.	Andrés	Pombal	Bombarral Fm.	Tooth
MNHNUL/AND.303	Diplodocoidea	Diplodocoidea indet.	Andrés	Pombal	Bombarral Fm.	Tooth
MNHNUL/AND.304	Diplodocoidea	Diplodocoidea indet.	Andrés	Pombal	Bombarral Fm.	Tooth
SHN (JJS) 121	?Macronaria	?Macronaria indet.	Cambelas	Torres Vedras	Freixial Fm.	Tooth
SHN (JJS) 127	? Turiasauria	?Turiasauria indet.	Valmitão Norte	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN (JJS) 128	? Turiasauria	?Turiasauria indet.	Praia dos Frades	Peniche	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN (JJS) 129	? Turiasauria	?Turiasauria indet.	Praia de Pedrogão	Peniche	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN (JJS) 130	? Turiasauria	?Turiasauria indet.	Praia de Pedrogão	Peniche	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN (JJS) 131	? Turiasauria	?Turiasauria indet.	Praia dos Frades	Peniche	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN (JJS) 132	? Turiasauria	?Turiasauria indet.	São Bernardino	Peniche	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN (JJS) 133	? Turiasauria	?Turiasauria indet.	Valmitão Norte	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN (JJS) 135	? Turiasauria	?Turiasauria indet.	Valmitão Norte	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN (JJS) 136	? Turiasauria	?Turiasauria indet.	Porto das Barcas	Lourinhã	Sobral Fm.	Tooth
SHN (JJS) 139	? Turiasauria	?Turiasauria indet.	Praia da Corva	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN (JJS) 140	? Turiasauria	?Turiasauria indet.	Cambelas	Torres Vedras	Freixial Fm.	Tooth
SHN (JJS) 141	? Turiasauria	?Turiasauria indet.	Baleal	Peniche	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN (JJS) 142	? Turiasauria	?Turiasauria indet.	Praia da Corva	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN (JJS) 146	? Turiasauria	?Turiasauria indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.	Tooth

Table S.1. List of the sauropod material from the Upper Jurassic of the Lusitanian Basin

Number	Taxonomy		Locality	Municipality	Horizon	Anatomy
SHN (JJS) 147	? Turiasauria	?Turiasauria indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.	Tooth
SHN (JJS) 148	? Turiasauria	?Turiasauria indet.	?	?	?	Tooth
SHN (JJS) 149	? Turiasauria	?Turiasauria indet.	?	?	?	Tooth
SHN (JJS) 151	? Turiasauria	?Turiasauria indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.	Tooth
SHN (JJS) 154	? Turiasauria	?Turiasauria indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.	Tooth
SHN (JJS) 177	Diplodocinae	Diplodocinae indet.	Valmitão	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Partial skeleton
SHN (JJS) 178	Diplodocidae	Diplodocidae indet.	Cambelas	Torres Vedras	Freixial Fm.	Partial skeleton
SHN (JJS) 179	Diplodocidae	Diplodocidae indet.	Praia da Areia Branca	Lourinhã	Bombarral Fm.	Partial skeleton
SHN 002	?Macronaria	?Macronaria indet.	Porto Novo	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Partial skeleton
SHN 006	Diplodocidae	Diplodocidae indet.	Mexeloeira	Torres Vedras	Bombarral Fm.	Axial elements
SHN 122	?Macronaria	?Macronaria indet.	Peralta Norte	Lourinhã	Sobral Fm.	Tooth
SHN 134	? Turiasauria	Turiasauria indet.	Valmitão	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 137	? Turiasauria	Turiasauria indet.	São Bernardino	Peniche	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 138	? Turiasauria	Turiasauria indet.	Porto Novo	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 143	? Turiasauria	Turiasauria indet.	Valmitão Norte	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 144	? Turiasauria	Turiasauria indet.	Porto Dinheiro	Lourinhã	Fm./Sobral Fm.	Tooth
SHN 145	? Turiasauria	Turiasauria indet.	Praia da Corva	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 150	? Turiasauria	Turiasauria indet.	Serra do Bouro	Caldas da Rainha	Bombarral Fm.	Tooth
SHN 152	? Turiasauria	Turiasauria indet.	Serra do Bouro	Caldas da Rainha	Bombarral Fm.	Tooth
SHN 153	? Turiasauria	Turiasauria indet.	Porto Dinheiro	Lourinhã	Fm./Sobral Fm.	Tooth
SHN 180	Eusauropoda	Eusauropoda indet.	Baleal	Peniche	Praia de Amoreira-Porto Novo Fm.	Anterior caudal vertebra
SHN 181	Macronaria	Macronaria indet	Valmitão	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Partial skeleton
SHN 501	? Turiasauria	Turiasauria indet.	Praia da Gralha	Alcobaça	Alcobaça Fm.	Tooth
SHN 502	? Turiasauria	Turiasauria indet.	Foz do Arelho	Caldas da Rainha	Bombarral Fm.	Tooth
SHN 503	? Turiasauria	Turiasauria indet.	Foz do Arelho	Caldas da Rainha	Bombarral Fm.	Tooth
SHN 504	? Turiasauria	Turiasauria indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.	Tooth
SHN 505	? Turiasauria	Turiasauria indet.	Valmitão Sul	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 506	? Turiasauria	Turiasauria indet.	Valmitão Norte	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 507	? Turiasauria	Turiasauria indet.	Valmitão Sul	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 508	? Turiasauria	Turiasauria indet.	Serra do Bouro	Caldas da Rainha	Bombarral Fm.	Tooth
SHN 509	? Turiasauria	Turiasauria indet.	Valmitão Sul	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 510	? Turiasauria	Turiasauria indet.	Praia da Corva	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 511	? Turiasauria	Turiasauria indet.	?	?	?	Tooth
SHN 512	? Turiasauria	Turiasauria indet.	Foz de Arelho	Caldas da Rainha	Bombarral Fm.	Tooth
SHN 513	?Macronaria	?Macronaria indet.	Porto Novo	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 514	?Macronaria	?Macronaria indet.	Serra do Bouro	Caldas da Rainha	Bombarral Fm.	Tooth
SHN 515	?Macronaria	?Macronaria indet.	Peralta Norte	Lourinhã	Sobral Fm.	Tooth
SHN 516	?Macronaria	?Macronaria indet.	Praia dos Frades-São Bernardino	Peniche	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 517	?Macronaria	?Macronaria indet.	Foz do Arelho	Caldas da Rainha	Bombarral Fm.	Tooth
SHN 518	?Macronaria	?Macronaria indet.	Peralta Norte	Lourinhã	Sobral Fm.	Tooth
SHN 519	?Macronaria	?Macronaria indet.	Sul da Foz do Rio Sizandro	Torres Vedras	Freixial Fm.	Tooth
SHN 520	Sauropoda	Sauropoda indet.	Praia dos Frades	Peniche	Praia de Amoreira-Porto Novo Fm.	Left femur
SHN 521	Diplodocinae	Diplodocinae indet.	Valmitão Norte	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Middle caudal vertebra
SHN 522	Sauropoda	Sauropoda indet.	Cambelas Sul	Torres Vedras	Freixial Fm.	Left pubis
SHN 523	Titanosauriformes	Titanosauriformes indet.	Praia da Corva	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Caudal vertebrae
SHN 524	Sauropoda	Sauropoda indet.	Praia de Pedrogãos	Peniche	Praia de Amoreira-Porto Novo Fm.	Ungueal I
SHN 525	Sauropoda	Sauropoda indet.	Valmitão	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Axial elements
SHN 526	Macronaria	Macronaria indet.	Baleal-Almagreira	Peniche	Bombarral Fm.	Right pubis

Table S.1. List of the sauropod material from the Upper Jurassic of the Lusitanian Basin

Number	Taxonomy		Locality	Municipality	Horizon	Anatomy
SHN 527	Sauropoda	Sauropoda indet.	Cambelas	Torres Vedras	Freixial Fm.	Right tibia
SHN 528	Eusauropoda	Eusauropoda indet.	Porto Barril	Mafra	Freixial Fm.	Middle cervical vertebrae
SHN 529	Camarasauridae	Camarasauridae indet.	Cambelas	Torres Vedras	Freixial Fm.	Partial skeleton (one or more individuals)
SHN 530	Eusauropoda	Eusauropoda indet.	Praia da Corva	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Partial skeleton (one or more individuals)
SHN 531	Camarasauridae	Camarasauridae indet.	Cambelas	Torres Vedras	Freixial Fm.	Partial skeleton
SHN 532	Eusauropoda	Eusauropoda indet.	Ponte de Rol	Torres Vedras	Sobral Fm.	Partial skeleton
SHN 533	Eusauropoda	Eusauropoda indet.	Praia Azul	Torres Vedras	Sobral Fm.	Partial skeleton
SHN 534	Sauropoda	Sauropoda indet.	Santa Rita	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Partial skeleton
SHN 535	Eusauropoda	Eusauropoda indet.	Praia do Seixo	Torres Vedras	Bombarral Fm.	?Cervical vertebra
SHN 536	Sauropoda	Sauropoda indet.	Pedras Muitas	Peniche	Praia de Amoreira-Porto Novo Fm.	Partial right ilium
SHN 537	Sauropoda	Sauropoda indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.	pedal element (+ indeterminate fragments)
SHN 538	Sauropoda	Sauropoda indet.	Almagreira	Peniche	Bombarral Fm.	Sacral ribs and indeterminate fragments
SHN 539	Sauropoda	Sauropoda indet.	Porto das Barcas	Lourinhã	Sobral Fm.	Axial and appendicular elements
SHN 540	?Macronaria	?Macronaria indet.	São Bernardino Norte	Peniche	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 541	?Macronaria	?Macronaria indet.	Sul Pedra da Ursa	Torres Vedras	Freixial Fm.	Tooth
SHN 542	Titanosauriformes	Titanosauriformes indet.	Porto Dinheiro Norte	Lourinhã	Fm./Sobral Fm.	Tooth
SHN 543	Titanosauriformes	Titanosauriformes indet.	Baleal	Peniche	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 544	Titanosauriformes	Titanosauriformes indet.	Peralta	Lourinhã	Sobral Fm.	Tooth
SHN 545	Titanosauriformes	Titanosauriformes indet.	Peralta	Lourinhã	Sobral Fm.	Tooth
SHN 546	Titanosauriformes	Titanosauriformes indet.	Praia Vermelha	Peniche	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 547	Titanosauriformes	Titanosauriformes indet.	Pedras Muitas	Peniche	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 548	Titanosauriformes	Titanosauriformes indet.	Valmitão Sul	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 549	Titanosauriformes	Titanosauriformes indet.	Praia Azul	Torres Vedras	Sobral Fm.	Tooth
SHN 550	Titanosauriformes	Titanosauriformes indet.	Peralta Norte	Lourinhã	Sobral Fm.	Tooth
SHN 551	Titanosauriformes	Titanosauriformes indet.	Peralta Centro	Lourinhã	Sobral Fm.	Tooth
SHN 552	Titanosauriformes	Titanosauriformes indet.	Peralta Centro	Lourinhã	Sobral Fm.	Tooth
SHN 553	Sauropoda	Sauropoda indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.	Tooth
SHN 554	Titanosauriformes	Titanosauriformes indet.	Almagreira	Peniche	Bombarral Fm.	Tooth
SHN 555	Sauropoda	Sauropoda indet.	Porto Novo	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 556	Titanosauriformes	Titanosauriformes indet.	Almagreira	Peniche	Bombarral Fm.	Tooth
SHN 557	Sauropoda	Sauropoda indet.	Praia de Pedrogãos	Peniche	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 558	Sauropoda	Sauropoda indet.	Praia de Pedrogãos	Peniche	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 559	Titanosauriformes	Titanosauriformes indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.	Tooth
SHN 560	Sauropoda	Sauropoda indet.	Cambelas Norte	Torres Vedras	Freixial Fm.	Tooth
SHN 561	Sauropoda	Sauropoda indet.	Praia das Amoeiras	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 562	Sauropoda	Sauropoda indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.	Tooth
SHN 563	Sauropoda	Sauropoda indet.	?	?	?	Tooth
SHN 564	Sauropoda	Sauropoda indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.	Tooth
SHN 565	Sauropoda	Sauropoda indet.	Praia da Corva	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 566	Sauropoda	Sauropoda indet.	Valmitão Norte	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 567	Sauropoda	Sauropoda indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.	Tooth
SHN 568	Sauropoda	Sauropoda indet.	Valmitão Sul	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 570	Sauropoda	Sauropoda indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.	Tooth
SHN 571	Sauropoda	Sauropoda indet.	Serra do Bouro	Caldas da Rainha	Bombarral Fm.	Tooth
SHN 572	Titanosauriformes	Titanosauriformes indet.	Porto Dinheiro Norte	Lourinhã	Fm./Sobral Fm.	Tooth
SHN 573	Titanosauriformes	Titanosauriformes indet.	Vale de Pombas	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 574	Titanosauriformes	Titanosauriformes indet.	Valmitão Norte	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 575	Titanosauriformes	Titanosauriformes indet.	Valmitão	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 576	Titanosauriformes	Titanosauriformes indet.	Porto das Barcas	Lourinhã	Sobral Fm.	Tooth

Table S.1. List of the sauropod material from the Upper Jurassic of the Lusitanian Basin

Number	Taxonomy		Locality	Municipality	Horizon	Anatomy
SHN 577	Titanosauriformes	Titanosauriformes indet.	Valmitão Sul	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 578	Titanosauriformes	Titanosauriformes indet.	Valmitão Sul	Lourinhã	Praia de Amoreira-Porto Novo Fm.	Tooth
SHN 579	Titanosauriformes	Titanosauriformes indet.	Peralta meio	Lourinhã	Sobral Fm.	Tooth
SHN 580	Titanosauriformes	Titanosauriformes indet.	Assenta	Torres Vedras	Freixial Fm.	Tooth
SHN 581	Titanosauriformes	Titanosauriformes indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.	Tooth
SHN 582	?Turiasauria	?Turiasauria indet.	Praia dos Frades	Peniche	Praia de Amoreira-Porto Novo Fm.	Maxilla fargment
SHN 583	Turiasauria	cf. Turiasauria	Praia dos Frades	Peniche	Praia de Amoreira-Porto Novo Fm.	Metacarpal I
SHN 584	Sauropoda	Sauropoda indet.	Assenta	Torres Vedras	Freixial Fm.	Humerus distal end
SHN 585	Sauropoda	Sauropoda indet.	Almagreira	Peniche	Bombarral Fm.	Cervical vertebrae remains
SHN 586	Sauropoda	Sauropoda indet.	Gentias Norte	Torres Vedras	Freixial Fm.	Partial femur
SHN 587	Eusauropoda	Eusauropoda indet.	Praia da Corva	Torres Vedras	Praia de Amoreira-Porto Novo Fm.	Distal chevron
SHN 588	Diplodocinae	Diplodocinae indet.	Porto Dinheiro	Lourinhã	Fm./Sobral Fm.	Posterior caudal vertebra
SHN 589	Diplodocinae	Diplodocinae indet.	Baleal	Peniche	Praia de Amoreira-Porto Novo Fm.	Posterior caudal vertebra
SHN 590	Eusauropoda	Eusauropoda indet.	Mexolhoeira	Torres Vedras	Bombarral Fm.	Two presacral vertebrae
unlabelled	Diplodocidae	Diplodocidae indet.	?	?	?	Anterior caudal vertebra
unlabelled	Camarasauridae and Turiasauria	Indeterteminate taxa	Andrés	Pombal	Bombarral Fm.	Teeth and postcranial material
unlabelled	Sauropoda	Sauropoda indet.	Chiqueda de Cima	Alcobaça	Alcobaça Fm.	Posterior caudal vertebra
unlabelled	Titanosauriformes	Titanosauriformes indet.	Ourém	Ourém	Alcobaça Fm.?	Tooth
unlabelled	Sauropoda	Sauropoda indet.	Porto das Barcas	Lourinhã	Sobral Fm.	Anterior caudal vertebra
unlabelled	Sauropoda	Sauropoda indet.	Porto das Barcas	Lourinhã	Sobral Fm.	Anterior caudal vertebra
MNHN/UL.Din.027	Eusauropoda	Eusauropoda indet.	Praia da Areia Branca	Lourinhã	Bombarral Fm.	Anterior caudal vertebra
unlabelled	Sauropoda	Sauropoda indet.	Praia da Areia Branca	Lourinhã	Bombarral Fm.	Anterior caudal vertebra
unlabelled	Sauropoda	Sauropoda indet.	São Mamede	Bombarral	Alcobaça Fm.	Humerus
unlabelled	Eusauropoda	Eusauropoda indet.	Vermoil	Pombal	Bombarral Fm.	Middle-to-posterior dorsal neural arch

*More unpublished material is referred in a list provided by Mateus (2005)

SHN	Sociedade de História Natural, Torres Vedras, Portugal (plus (JJS) for the José Joaquim collection deposited in the Sociedade de História Natural)
MNHN/UL	Museu Nacional de História Natural e da Ciência, Universidade de Lisboa, Lisboa, Portugal
ML	Museu da Lourinhã, Lourinhã, Portugal
MG	Museu Geológico, Lisboa, Portugal
MMB.PALEO	Museu Municipal do Bombarral, Bombarral, Portugal (plus PALEO for the paleontological collection)
MMLT	Museu Municipal de Leonel Trindade, Torres Vedras, Portugal
MMPM	Museu Municipal de Porto de Mós, Porto de Mós, Portugal
GeoFCUL(AB)	Departamento de Geologia da Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal (plus AB for Areia Branca)

Table S.1. List of the sauropod material from the Upper Jurassic of the Lusitanian Basin

SUPPLEMENTARY MATERIAL 2

List of the sauropod material housed in Museu Geológico

Anatomy	Number	Taxonomy		Locality	Municipality	Horizon
Anterior caudal vertebra	MG 30483	Eusauropoda	Eusauropoda indet.	?	?	?
Partial skeleton	MG 4956, 30373, 30377, 30379, 4956, 30378, 30384, 30370, 4956, 30380, 30376, 4956, 30374, 30388, 30387, 5780, 30371, 5780, 30372, 30383, 30382, 2, 30381, 4979, 4979, 30385, 5781, 4975, 4970, 4957, 4931, 4983, 4984, 30375, 30386 and unlabelled fragmentary elements	Camarasauridae	*Lourinhasaurus alenquerensis*	Moinho do Carmo	Alenquer	Sobral Fm.
Partial humeral distal end	MG 20484	Sauropoda	Sauropoda indet.	?	Alenquer?	?
Pubic peduncle of an ilium	MG 30485	Titanosauriformes	Titanosauriformes indet.	Moinho do Carmo?	Alenquer?	Sobral Fm.?
Axial and apendicular elements	MG 30389	Sauropoda, Diplodocidae	Sauropoda indet. and Diplodocinae indet.	Batalha	Batalha	Alcobaça or Bombarral Fm.
Cervical or dorsal neural spine	MG 4920	Eusauropoda	Eusauropoda indet.	Monte da Cruz do Facho, Foz do Arelho	Caldas da Rainha	Bombarral Fm.
Middle caudal vertebra	MG 4804	Eusauropoda	Eusauropoda indet.	Casal de Lã, Salir de Matos	Caldas da Rainha	Bombarral Fm.
Tooth	MG 4832	?Turiasauria	?Turiasauria indet.	São Martinho do Porto	Caldas da Rainha	Alcobaça Fm.
Three partial middle/posterior caudal vertebrae	MG 4819, 4821, 4826	Diplodocinae	Diplodocinae indet.	São Gregório da Fanadia	Caldas da Rainha	Bombarral Fm.
Posterior caudal vertebra	MG 8799	Sauropoda	Sauropoda indet.	Praia das Almoinhas?	Caldas da Rainha or Torres Vedras?	Bombarral Fm.?
Partial dorsal vertebra and a partial caudal series	MG 4974	Sauropoda	Sauropoda indet.	Abadia (northern of Batalha)	Leiria	Alcobaça Fm.
Teeth	MG 27890-92, 27894, 27895	Titanosauriformes	Brachiosauridae indet.	Guimarota mine	Leiria	Alcobaça Fm.
Partial skeleton	MG 3794, 4798, 4801, 4805-10, 4838, 4944, 4950, 4952, 4958, 4964, 4965, 4966, 4981, 4982, 4803, 4985-1, 4985 2-20, 5795, 8793, 8794, 8807 and unlabeled sacral neural spine and chevron	Brachiosauridae	*Lusotitan atalaiensis*	Peralta	Lourinhã	Sobral Fm.
Middle caudal vertebrae	MG 8800	Eusauropoda	Eusauropoda indet.	Porto das Barcas	Lourinhã	Sobral Fm.
Middle caudal vertebra	MG 8805	Sauropoda	Sauropoda indet.	Porto das Barcas	Lourinhã	Sobral Fm.
Left femur	MG 4986	Titanosauriformes	Titanosauriformes indet	Praia da Areia Branca	Lourinhã	Bombarral Fm.
Right humerus	MG 4976	Eusauropoda	cf. *Duriatitan humerocristatus*	Praia dos Frades	Lourinhã	Praia de Amoreira-Porto Novo Fm.

Table S.2. List of the sauropod material housed in Museu Geológico

Three neural arch fragments	MG 8809	Sauropoda	Sauropoda indet.	Atalaia	Lourinhã	Sobral Fm.
Dorsal rib fragments	MG 30480	Sauropoda	Sauropoda indet.	Outeiro do Seixo, Ribamar	Lourinhã	Praia de Amoreira-Porto Novo Fm.
Four anterior and middle caudal vertebrae plus indeterminate fragments	MG 30390	Eusauropoda	Sauropoda indet.	Porto das Barcas	Lourinhã	Sobral Fm.
Two teeth fragments associated with "*Omasaurus lenieri*" material	MG 8771	Sauropoda	Sauropoda indet.	Porto das Barcas	Lourinhã	Sobral Fm.
Two dorsal rib fragments	MG 8792	Sauropoda	Sauropoda indet.	Atalaia	Lourinhã	Sobral Fm.
Right fibula	MG 30486	Eusauropoda	Turiasauria indet.	Atouguia da Baleia?	Lourinhã?	Praia de Amoreira-Porto Novo Fm.?
Partial dorsal centrum	MG 30482	Neosauropoda	Neosauropoda indet.	Atalaia?	Lourinhã?	Sobral Fm.?
Caudal neural spine	MG 30481	Sauropoda	Sauropoda indet.	Atalaia?	Lourinhã?	Sobral Fm.?
Tooth	MG 125	Titanosauriformes	Titanosauriformes indet.	Ourém	Ourém	Alcobaça Fm.?
Tooth	MG 16	?Turiasauria	?Turiasauria indet.	Ourém	Ourém	Alcobaça Fm.?
Cervical vertebrae remains	MG 4915, 4916, 4917, 4919	Diplodocidae	Diplodocidae indet	Pedras Muitas	Peniche	Bombarral Fm.
16 anterior to middle caudal vertebrae	MG 4978	Eusauropoda	Eusauropoda indet.	São Bernardino	Peniche	Praia de Amoreira-Porto Novo Fm.
Tooth	MG 8783	Eusauropoda	Eusauropoda indet.	Baleal	Peniche	Praia de Amoreira-Porto Novo Fm.
Middle/posterior caudal vertebra	MG 4811	Sauropoda	Sauropoda indet.	Albergaria dos Doze	Pombal	Bombarral Fm.
Anterior caudal vertebra	MG 4800	Sauropoda	Sauropoda indet.	Porto Novo	Torres Vedras	Praia de Amoreira-Porto Novo Fm.
Middle caudal vertebra	MG 4802	Sauropoda	Sauropoda indet.	Alto da Vela, Santa Cruz	Torres Vedras	Praia de Amoreira-Porto Novo Fm.
Caudal, ribs and an indeterminate fragment	MG 25197.1-6	Diplodocinae	Diplodocinae indet.	Porto Novo	Torres Vedras	Praia de Amoreira-Porto Novo Fm.
Middle caudal vertebra	MG 8804	Titanosauriformes	cf. *Lusotitan atalaiensis*	Maceira	Torres Vedras	Freixial Fm.
Partial caudal vertebra and indeterminate fragments	MG 25254.2-4	Sauropoda	Sauropoda indet.	Between Foz Velha da Maceira and Cambelas	Torres Vedras	Freixial Fm.
Partial tibial distal end	MG 8803	Sauropoda	Sauropoda indet.	Serra da Vila	Torres Vedras	Sobral Fm.
Middle/posterior dorsal vertebra	MG 4799	Neosauropoda	Neosauropoda indet.	Castanheira	Vila Franca de Xira	Abadia Fm.
Middle caudal vertebra	MG 8802	Sauropoda	Sauropoda indet.	?	?	?
Tooth	MG277	?Turiasauria	?Turiasauria indet.	Fervença	Alcobaça	Alcobaça Fm.
Tooth fragment	MG 8772	Titanosauriformes	Titanosauriformes indet.	Praia da Areia Branca	Lourinhã	Bombarral Fm.

Table S.2. List of the sauropod material housed in Museu Geológico

SUPPLEMENTARY MATERIAL 3

Measurements of some sauropod specimens housed in Museu Geológico

Measurement	CdA	CdB	CdC	CdD	CdE	CdF	CdG	CdH	CdI	CdJ	CdK	CdL	CdM	CdN	CdO
centrum anteroposterior width	18	17,2	16,6	17,4	16,8	16,4	16,1	15,2	15,2	15,4	14,8	15,2	15,3	14,5	14,2
mediolateral width of the anterior articulation	?	?	?	?	24.5	21	17,2	16.9	?	15,2	15,2	15	14,9	14,8	14,1
dorsoventral width of the anterior articulation	23,8	?	18	?	19	18,6	19.3	17,1	?	15,1	14,5	13,9	?	12,6	12,2
mediolateral width of the posterior articulation	24	24,2	24,4	23,2	22,5	16	17,6	16	16,2	15,2	15,1	15,1	14,8	14,1	13
dorsoventral width of the posterior articulation	20,1	17,8	17.4	17,9	17,6	20,1	18.5	?	15.2	14,3	14,2	13,6	12,2	11	11,1

Mediolateral length does not consider the lateral projection of the lateral crests of the centrum, and the dorsoventral width of the articulation excludes the contribution of the chevron facets. The measurements are in cm.

Table S.3. Measurements of some sauropod specimens housed in Museu Geológico: São Bernardino tail (MG 4983)

Measurement	MG 8804	MG 8800	MG 8805**	MG 4802	MG 4800	MG 4804	MG 4821	MG 4826
centrum anteroposterior width	16,1	13,8	15,4	12,67	11,6	12,5	?	?
mediolateral width of the anterior articulation	17,1	15,1	13,3	11,5	20,2	14,2	14,2	?
dorsoventral width of the anterior articulation	12,5	11,7	11*	9,15	18,2	13	12,4	?
mediolateral width of the posterior articulation	?	?	13,5	11,3	18,9	13,4	?	13,3
dorsoventral width of the posterior articulation	?	12,1	11*	8,9	17,4	12,1	?	11,5

**approximate*

***appreciable deformation*

Table S.4. Measurements of some sauropod specimens housed in Museu Geológico: Other caudal vertebrae housed in Museu Geológico I

Measurement	MG 4819	MG 25254.2	MG 4811	MG 8799	MG 25197.4	MG 25197.5	MG 25197.6
centrum anteroposterior width	?	?	13,9	?	?	?	?
mediolateral width of the anterior articulation	?	?	9,7	?	?	?	?
dorsoventral width of the anterior articulation	?	?	8,6	?	?	?	?
mediolateral width of the posterior articulation	14,1	11,5	?	10*	?	?	?
dorsoventral width of the posterior articulation	13,5	?	8,2	8,1	?	?	?

**approximate*

***appreciable deformation*

Table S.5. Measurements of some sauropod specimens housed in Museu Geológico: Other caudal vertebrae housed in Museu Geológico II

Measurements	MG 4986
total length	?
proximal end mediolateral width	167
femoral head anteroposterior width	?
minimum diameter of diaphysis	15*
maximum diameter of diaphysis	41,5*
distal end mediolateral width	?
tibial condyle anteroposterior width	?
fibular condyle anteroposterior width	?

** The diaphysis is not complete, and the section with the minimum diameter is unknown*

Table S.6. Measurements of some sauropod specimens housed in Museu Geológico: Praia da Areia Branca Femur (MG 4986)

Measurement	MG 4976
total length	?
proximal end anteroposterior width	?
humeral head anteroposterior width	?
minimum diameter of diaphysis	13
maximum diameter of diaphysis	17,8
distal end anteroposterior width	?
distal end mediolateral width	?

Table S.7. Measurements of some sauropod specimens housed in Museu Geológico: Praia dos Frades humerus (MG 4976)

SUPPLEMENTARY MATERIAL 4

Measurements of spatulate-, compressed cone-chisel- and peg-shaped teeth

Tooth	Locality	Formation*	Age*	Wear	Max. height	Width at the base	Width at apex base	Max height of apex	Height apex/total height	SI	LOG SI
SHN 122	Peralta Norte	Sobral Fm.	upper Kimmeridgian-Tithonian	absent/weak	46,35	25	29,9	17,65	0,381	1,550	0,190
SHN (JJS) 121	Cambelas	Freixial Fm.	Tithonian	absent/weak	?	?	?	9,9	?	?	?
SHN 513	Porto Novo	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-Tithonian	moderate	39,05	25,1	26,75	13,6	0,348	1,460	0,164
SHN 514	Serra do Bouro	Bombarral Fm.	Tithonian	?	?	?	17,85	?	?	?	?
SHN (JJS) 515	Peralta Norte	Sobral Fm.	upper Kimmeridgian-Tithonian	moderate	?	?	?	?	?	?	?
SHN 516	Praia dos Frades-São Bernardino	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-Tithonian	?	?	?	?	?	?	?	?
SHN 517	Foz do Arelho	Bombarral Fm.	Tithonian	moderate	?	15,5	18,4		?	?	?
SHN (JJS) 518	Peralta Norte	Sobral Fm.	upper Kimmeridgian-Tithonian	?	?	?	?	?	?	?	?
SHN (JJS) 519	Sul da Foz do Rio Sizandro	Freixial Fm.	Tithonian	moderate	44,5	19,4	22,85	18,3	0,411	1,947	0,289
SHN (JJS) 540	São Bernardino Norte	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-Tithonian	moderate	?	10,15	11,6	?	?	?	?
SHN 541	Sul Pedra da Ursa	Freixial Fm.	Tithonian	moderate	?	17,1	19,4	?	?	?	?
MG 3783	Baleal	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-Tithonian		?	?	?	?	?	?	?
									avg	1,652	0,215
									min	1,460	0,164
									max	1,947	0,289
									sd	0,212	0,054

Table S.8. Measurements for spatulate-shaped teeth of Lusitanian Basin

Tooth	Locality	Formation*	Age*	Wear	Max. height	Width at the base	Width at apex base	Max height of apex	Height apex/total height	SI	LOG SI
SHN 542	Porto Dinheiro Norte	Sobral Fm.	upper Kimmeridgian-Tithonian	Strong	?	16,5**	15,5	13,45	?	?	?
SHN 543	Baleal	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-Tithonian	absent/weak	44,4*	15,85**	16,7	23	0,518*	2,801*	0,447*
SHN (JJS) 544	Peralta	Sobral Fm.	upper Kimmeridgian-Tithonian	absent/weak	?	?	?	?	?	?	?
SHN (JJS) 545	Peralta	Sobral Fm.	upper Kimmeridgian-Tithonian	absent/weak	?	?	?	?	?	?	?
SHN 546	Praia da Vermelha	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-Tithonian	?	?	13,9	14,95	?	?	?	?
SHN 547	Pedras Muitas	Praia de Amoreira-Porto Novo Fm./Bombarral Fm.	upper Kimmeridgian-Tithonian	moderate	?	14,45	?	?	?	?	?
SHN (JJS) 550	Peralta Norte	Sobral Fm.	upper Kimmeridgian-Tithonian	absent/weak	61,2	18,8	21,3	24,8	0,405	3,255	0,513
SHN (JJS) 551	Peralta Centro	Sobral Fm.	upper Kimmeridgian-Tithonian	moderate	?	?	18,3	19,5	?	?	?
SHN (JJS) 552	Peralta Centro	Sobral Fm.	upper Kimmeridgian-Tithonian	?	?	?	?	?	?	?	?
SHN 554	Almagreira	Bombarral Fm.	Tithonian	absent/weak	44,65	16,65	17,65	26,35	0,590	2,682	0,428
SHN 556	Almagreira	Bombarral Fm.	Tithonian	moderate	?	?	12,95	9,5	?	?	?
SHN (JJS) 559	Salir do Porto	Alcobaça Fm.	Lower Kimmeridgian	?	?	?	?	?	?	?	?
SHN (JJS) 572	Porto Dinheiro Norte	Sobral Fm.	upper Kimmeridgian-Tithonian	absent/weak	?	?	8,3	11,8	?	?	?
MG 8772	Praia da Areia Branca	Bombarral Fm.	Tithonian	moderate	?	?	?	?	?	?	?
MG 8772	Praia da Areia Branca	Bombarral Fm.	Tithonian	moderate	?	?	?	?	?	?	?
									avg	2,969	0,471
									min	2,682	0,428
									max	3,255	0,513
									sd	0,287	0,042

Table S.9. Measurements for the morphotype I of compressed cone-chisel-shaped teeth of Lusitanian Basin

Tooth	Locality	Formation*	Age*	Wear	Max. height	Width at the base	Width at apex base	Max height of apex	Height apex/total height	SI	LOG SI
SHN (JJS) 549	Praia Azul	Sobral Fm.	Tithonian	?	?	10	?	?	?	?	?
MG 27891	Guimarota	Alcobaça Fm.	Kimmeridgian-Lower Tithonian	absent/weak	26	7,7	9	13,1	0,504	3,377	0,528
MG 27892	Guimarota	Alcobaça Fm.	Kimmeridgian-Lower Tithonian	?	?	6,4	9	?	?	?	?
MG 27894	Guimarota	Alcobaça Fm.	Kimmeridgian-Lower Tithonian	?	?	6,6	8,7	?	?	?	?
MG 27895	Guimarota	Alcobaça Fm.	Kimmeridgian-Lower Tithonian	?	?	7,8	?	?	?	?	?
MG 8779	Ourém	Montejunto or Alcobaça Fm.	middle-to-upper Oxfordian or Kimmeridgian-basal Tithonian	?	42,5	13,93	16,9	19,1	0,449	3,051	0,484
									avg	3,214	0,506
									min	3,051	0,484
									max	3,377	0,528
									sd	0,163	0,022

Table S.10. Measurements for the morphotype II of compressed cone-chisel-shaped teeth of Lusitanian Basin

Tooth	Locality	Formation*	Age*	Wear	Max. height	Width at the base	Width at apex base	Max height of apex	Height apex/total height	SI	LOG SI
SHN (JJS) 573	Vale de Pombas	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-Tithonian	absent/weak	?	?	8,45	12,6	?	?	?
SHN 574	Valmitão Norte	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-Tithonian	absent/weak	?	?	9,5	14,5	?	?	?
SHN 575	Valmitão	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-Tithonian	?	?	8,3	9,05	?	?	?	?
SHN (JJS) 576	Porto das Barcas	Sobral Fm.	upper Kimmeridgian-Tithonian	absent/weak	?	?	?	?	?	?	?
SHN (JJS) 577	Valmitão Sul	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-Tithonian	absent/weak	?	?	?	?	?	?	?
SHN 578	Valmitão Sul	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-Tithonian	moderate?	19,45	5,6	6,45	5,5	0,283	3,473	0,541
SHN (JJS) 579	Peralta meio	Sobral Fm.	upper Kimmeridgian-Tithonian	?	?	7,2	?	?	?	?	?
SHN 580	Assenta	Freixial Fm.	Tithonian	moderate	15,45	5,85	6,3	3,7	0,239	2,641	0,422
SHN 581	Salir do Porto	Alcobaça Fm.	lower Kimmeridgian	?	?	?	?	?	?	?	?
SHN (JJS) 548	Valmitão Sul	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-Tithonian	moderate	21,35*	7,6**	7	5,9	0,276*	2,809*	0,448*
									avg	3,057	0,481
									min	3,473	0,541
									max	3,473	0,541
									sd	0,000	0,000

Table S.11. Measurements for the morphotype III of compressed cone-chisel-shaped teeth of Lusitanian Basin

Tooth	Locality	Formation*	Age*	Wear	Max. height	Width at the base	Width at apex base	Max height of apex	Height apex/total height	SI	LOG SI
MNHNUL/AND 302	Andrés	Bombarral Fm.	Tithonian	moderate	0,87	0,22	0,24	?	?	3,955	0,597
MNHNUL/AND 303	Andrés	Bombarral Fm.	Tithonian	absent/weak	1,93	0,74	0,55	?	?	2,608	0,416
MNHNUL/AND 304	Andrés	Bombarral Fm.	Tithonian	moderate	1,13	0,3	0,24	?	?	3,767	0,576
									avg	3,861	0,587
									min	3,767	0,576
									max	3,955	0,597
									sd	0,094	0,011

Table S.12. Measurements for compressed peg-shaped teeth of Lusitanian Basin

SUPPLEMENTARY MATERIAL 5

List of the sauropod material from central and northern part of the Bombarral Sub-basin

Anatomy	Number	Taxonomy		Locality	Municipality	Formation
Tooth	MG 125	Titanosauriformes	Titanosauriformes	Ourém	Ourém	?
Tooth	MG 16	?Turiasauria	?Turiasauria indet.	Ourém	Ourém	?
Tooth	MG 277	?Turiasauria	?Turiasauria indet.	Fervença	Alcobaça	Alcobaça Fm.
Teeth	MG 27890-92, 27894, 27895	Titanosauriformes	Brachiosauridae indet.	Guimarota mine	Leiria	Alcobaça Fm.
Axial and apendicular elements	MG 30389	Sauropoda, Diplodocidae	Sauropoda indet. and Diplodocinae indet.	Batalha	Batalha	Alcobaça or Bombarral Fm.
Middle caudal vertebra	MG 4804	Sauropoda	Sauropoda indet.	Casal de Lã, Salir de Matos	Caldas da Rainha	Bombarral Fm.
Three partial middle/posterior caudal vertebra	MG 4819, 4821, 4826	Diplodocinae	Diplodocinae indet.	São Gregório da Fanadia	Caldas da Rainha	Bombarral Fm.
Tooth	MG 4832	?Turiasauria	?Turiasauria indet.	São Martinho do Porto	Alcobaça	Alcobaça Fm.
Cervical or dorsal neural spine	MG 4920	Eusauropoda	Eusauropoda indet.	Monte da Cruz do Facho, Foz do Arelho	Caldas da Rainha	Bombarral Fm.
Partial dorsal vertebra and a partial caudal series	MG 4974	Sauropoda	Sauropoda indet.	Abadia (northern of Batalha)	Leiria	Alcobaça Fm.
Posterior caudal vertebra	MG 4811	Sauropoda	Sauropoda indet.	Albergaria dos Doze	Pombal	Bombarral Fm.
Posterior caudal vertebra	MG 8799	Sauropoda	Sauropoda indet.	Praia das Almoinhas?	Caldas da Rainha or Torres Vedras?	Bombarral Fm.?
Imcomplete femur, proximal end	MMPM.P/307	Sauropoda	Sauropoda indet.	Golfeiros	Batalha	Alcobaça Fm.
Middle caudal vertebra and a chevron distal end	MMPM.P/551	Eusauropoda	Eusauropoda indet.	São Martinho do Porto	Alcobaça	Alcobaça Fm.
Posterior caudal vertebra	MMPM.P/554	Sauropoda	Sauropoda indet.	Fonte do Oleiro	Porto de Mós	Alcobaça Fm.
Appendicular bone	MMPM.P/587	Sauropoda	Sauropoda indet.	São Martinho do Porto	Alcobaça	Alcobaça Fm.
Posterior caudal vertebra	MMPM.P/587	Sauropoda	Sauropoda indet.	Albergaria	Porto de Mós	Bombarral or Alcobaça Fm.
Appendicular bone	MMPM.P/72	Sauropoda	Sauropoda indet.	Malásia	Caldas da Rainha	Bombarral Fm.
Left astragalus	MMPM.P/75	Eusauropoda	Eusauropoda indet.	Imaginário	Caldas da Rainha	Bombarral Fm.
Tooth	SHN (JJS) 146	?Turiasauria	?Turiasauria indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.
Tooth	SHN (JJS) 147	?Turiasauria	?Turiasauria indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.
Tooth	SHN (JJS) 151	?Turiasauria	?Turiasauria indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.
Tooth	SHN (JJS) 154	?Turiasauria	?Turiasauria indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.
Tooth	SHN (JJS) 504	?Turiasauria	?Turiasauria indet.	Salir do Porto	Caldas da Rainha	Alcobaça Fm.
Tooth	SHN 150	?Turiasauria	?Turiasauria indet.	Serra do Bouro	Caldas da Rainha	Bombarral Fm.
Tooth	SHN 152	?Turiasauria	?Turiasauria indet.	Serra do Bouro	Caldas da Rainha	Bombarral Fm.
Tooth	SHN 501	?Turiasauria	?Turiasauria indet.	Praia da Gralha	Alcobaça	Alcobaça Fm.
Tooth	SHN 502	?Turiasauria	?Turiasauria indet.	Foz do Arelho	Caldas da Rainha	Bombarral Fm.
Tooth	SHN 503	?Turiasauria	?Turiasauria indet.	Foz do Arelho	Caldas da Rainha	Bombarral Fm.
Tooth	SHN 508	?Turiasauria	?Turiasauria indet.	Serra do Bouro	Caldas da Rainha	Bombarral Fm.
Tooth	SHN 512	?Turiasauria	?Turiasauria indet.	Foz de Arelho	Caldas da Rainha	Bombarral Fm.
Middle or posterior dorsal neural spine	unlabelled	Eusauropoda	Eusauropoda indet.	Vermoil	Pombal	Bombarral Fm.
More than 20 teeth	unlabelled	Turiasauria, Titanosauriformes and Diplodocoidea	Turiasauria indet., Titanosauriformes indet. and Diplodocoidea indet.	Andrés	Pombal	Bombarral Fm.
unprepared post-axial elements	unlabelled	Sauropoda	Sauropoda indet.	Andrés	Pombal	Bombarral Fm.

Table S.13. List of the sauropod material from the central and northern part of the Bombarral Sub-basin

SUPPLEMENTARY MATERIAL 6

Measurements of the sauropod material from central and northern part of the Bombarral Sub-basin

Measurements	Cau-1*	Cau-2*	Cau-3*	Cau-4*	Cau-5*	Cau-6*	Cau-7*	Cau-8*	Cau-9*
centrum anteroposterior width	107	114	119	117	124	116	121	122	126
mediolateral width of the anterior articulation	177?	175	?	154	?	?	120	116	?
dorsoventral width of the anterior articulation	?	163	154	?	?	130	126	?	111
mediolateral width of the posterior articulation	177	163	?	145	130	124	118	113	118
dorsoventral width of the posterior articulation	165	152	?	?	?	130	127	122	106

Measurements in mm

Table S.14. Measurements of the sauropod material from central and northern part of the Bombarral Sub-basin: Abadia tail (MG 4974)

Measurement	MMPM.P/551	MMPM.P/554
centrum anteroposterior width	13,2	11,8
mediolateral width of the anterior articulation	11,4	8,7
dorsoventral width of the anterior articulation	10,2	8,6
mediolateral width of the posterior articulation	?	9,5
dorsoventral width of the posterior articulation	?	8,7

Measurements in cm

Table S.15. Measurements of the sauropod material from central and northern part of the Bombarral Sub-basin: MMPM.P/551 and MMPM.P/554

Measurement	dorsal centrum	caudal centrum
centrum anteroposterior width	?	?
mediolateral width of the anterior articulation	24,6	?
dorsoventral width of the anterior articulation	23,8*	?
mediolateral width of the posterior articulation	?	20,5
dorsoventral width of the posterior articulation	?	?

**approximate*
Measurements in cm

Table S.16. Measurements of the sauropod material from central and northern part of the Bombarral Sub-basin: MG 30389

Measurement	unlabeled specimen
transverse with of the neural spine	14,2
height of the neural spine from the postzygapophyses	23,5

Measurements in cm

Table S.17. Measurements of the sauropod material from central and northern part of the Bombarral Sub-basin: Vermoil dorsal neural spine

Measurements	MMPM.P/75
maximum anteroposterior width	18
Maximum mediolateral width	36
height on ascending process of astragalus	19,8

Measurements in cm

Table S.18. Measurements of the sauropod material from central and northern part of the Bombarral Sub-basin: astragalus of MMPM.P/75

SUPPLEMENTARY MATERIAL 7

Measurements of heart-shaped teeth

Tooth	Locality	Formation*	Age*	Wear	Morphotype	max. height	Width at the base	Width at apex base	Max height of apex	Height apex/total height	SI	LOG SI
SHN (JJS) 127	Valmitão Norte	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	moderate	III or II	28,80	19,50	23,90	15,16	0,526	1,205	0,08099
SHN (JJS) 128	Praia dos Frades	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	absent/weak	III	29,00	?	26,00	7,90	0,272	1,115	0,04742
SHN (JJS) 129	Praia de Pedrogãos	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	strong	?	28,59	?	?	13,10	0,458	?	?
SHN (JJS) 130	Praia de Pedrogãos	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	strong	II	19,11	11,00	17,10	7,00	0,366	1,118	0,04826
SHN (JJS) 131	Praia dos Frades	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	moderate	I	41,45	22,70	27,00	22,15	0,534	1,535	0,18616
SHN (JJS) 132	São Bernardino	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	moderate	I	39,35	27,30	28,00	20,85	0,530	1,405	0,14779
SHN (JJS) 133	Valmitão Norte	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	absent/weak	I	43,75	?	?	?	?	?	?
SHN (JJS) 135	Valmitão Norte	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	moderate	II	35,35	19,45	26,80	18,60	0,526	1,319	0,12025
SHN (JJS) 136	Porto das Barcas	Sobral Fm.	lower Tithonian	moderate	?	?	?	25,00	18,50	?	?	?
SHN (JJS) 139	Praia da Corva	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	moderate	III	42,90	22,2	32,90	12,60	0,294	1,304	0,11526
SHN (JJS) 140	Cambelas	Freixial Fm.	Tithonian	absent/weak to moderate	I	46,11	21,00	25,50	28,00	0,607	1,808	0,25725
SHN (JJS) 141	Baleal	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	moderate	II	32,90	16,95	23,60	13,90	0,422	1,394	0,14428
SHN (JJS) 142	Praia da Corva	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	absent/weak	I	41,95	22,30	26,99	24,30	0,579	1,554	0,19153
SHN (JJS) 146	Salir do Porto	Alcobaça Fm.	lower Kimmeridgian	absent/weak	III	?	?	?	?	?	?	?
SHN (JJS) 147	Salir do Porto	Alcobaça Fm.	lower Kimmeridgian	absent/weak	II	35,20	18,80	24,70	17,00	0,483	1,425	0,15385
SHN (JJS) 148	?	?	?	moderate	II	32,25	15,90	22,80	12,50	0,388	1,414	0,15059
SHN (JJS) 149	?	?	?	strong	III	25,4	17,90	23,90	7,50	0,295	1,063	0,02644
SHN (JJS) 151	Salir do Porto	Alcobaça Fm.	lower Kimmeridgian	moderate	?	?	?	?	?	?	?	?
SHN (JJS) 154	Salir do Porto	Alcobaça Fm.	lower Kimmeridgian	absent/weak	?	?	?	?	?	?	?	?
SHN (JJS) 504	Salir do Porto	Alcobaça Fm.	lower Kimmeridgian	absent/weak	?	?	?	?	?	?	?	?
SHN 134	Valmitão	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	absent/weak	?	?	?	?	?	?	?	?
SHN 137	São Bernardino	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	absent/weak	III	24,30	15,25	19,70	6,40	0,263	1,234	0,09114

Table S.19. Measurements of heart-shaped teeth of the Lusitanian Basin

SHN 138	Porto Novo	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	absent/weak	II	37,00	23.3	26,00	16,95	0,458	1,423	0,15323
SHN 143	Valmitão Norte	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	moderate	?	36,00	16,90	25,60	17,50	0,486	1,406	0,14806
SHN 144	Porto Dinheiro	Sobral Fm.	upper Kimmeridgian-lower Tithonian	absent/weak	II	32,10	15,90	24,10	15,00	0,467	1,332	0,12449
SHN 145	Praia da Corva	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	moderate (?)	II	?	24,40	29,90	?	?	?	?
SHN 150	Serra do Bouro	Bombarral Fm.	Tithonian	moderate	II	?	?	23,95	?	?	?	?
SHN 152	Serra do Bouro	Bombarral Fm.	Tithonian	moderate	I or II	28,6	14,30	17,20	13,10	0,458	1,663	0,22084
SHN 153	Porto Dinheiro	Sobral Fm.	upper Kimmeridgian-lower Tithonian	absent/weak	II	25,30	?	?	9,10	0,360	?	?
SHN 501	Praia da Gralha	Alcobaça Fm.	lower Kimmeridgian	moderate	I	?	?	?	?	?	?	?
SHN 502	Foz do Arelho	Bombarral Fm.	Tithonian	absent/weak	I	32,6	?	?	17,2	0,528	?	?
SHN 503	Foz do Arelho	Bombarral Fm.	Tithonian	moderate	II	32,3	20,7	24,9	19,1	0,591	1,297	0,11300
SHN 505	Valmitão Sul	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	absent/weak	III(?)	?	?	?	?	?	?	?
SHN 506	Valmitão Norte	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	moderate to strong	II	?	?	?	15,4	?	?	?
SHN 507	Valmitão Sul	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	moderate	?	?	?	?	?	?	?	?
SHN 508	Serra do Bouro	Bombarral Fm.	Tithonian	absent/weak	II	33,5	18,35	25	14,95	0,446	1,340	0,12710
SHN 509	Valmitão Sul	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	absent/weak	II	20,1	8,65	15,2	8,6	0,428	1,322	0,12135
SHN 510	Praia da Corva	Praia de Amoreira-Porto Novo Fm.	upper Kimmeridgian-basal Tithonian	strong	?	?	?	28,45	11,8	?	?	?
SHN 511	?	?	?	?	II	?	?	27,3	?	?	?	?
SHN 512	Foz de Arelho	Bombarral Fm.	Tithonian	absent/weak	II	19,1	8,65	12,95	7,65	0,401	1,475	0,16876
MG 4832	São Martinho do Porto	Alcobaça Fm.	lower Kimmeridgian	moderate	II	34	18	23	?	?	1,478	0,16975
MG 277	Fervença		lower Kimmeridgian	?	?	?	21	24	?	?	?	?
MG 16	Ourém	Montejunto or Alcobaça Fm.	middle-to-upper Oxfordian or Kimmeridgian-basal Tithonian	?	?	?	?	?	?	?	?	?

*(*sensu* Manuppella et al., 1999; Kullberg et al., 2006; Azerêdo et al., 2010)

Table S.19. Measurements of heart-shaped teeth of the Lusitanian Basin

SUPPLEMENTARY MATERIAL 8

SI values table

For more supplementary manterial see Mocho et al. (in press). This information was modified from the data provided Chure et al. (2010) and D'Emic et al. (2013)

	Sauropodomorpha	Diplodocoidea	Brachioisauriade	Euhelopodidae	Lithostrotia	Turiasauria-like	Mamenchisauridae	Basal eusauropod*
average	0,328	0,645	0,385	0,552	0,615	0,138	0,357	0,220
min	0,000	0,520	0,236	0,342	0,433	0,047	0,102	0,000
max	0,810	0,759	0,512	0,800	0,810	0,257	0,477	0,456
sd	0,158	0,060	0,068	0,132	0,095	0,047	0,099	0,104
species numb	80	8	6	3	11	1	4	9

*Basal eusauropods not including neosauropods, mamenchisaurids and putative eusauropods with problematic phylogeny such as *Datousaurus* .

References

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D'Emic MD, Mannion PD, Upchurch P, Benson RBJ, Pang Q, Zhengwu C. 2013. Osteology of *Huabeisaurus allocotus* (Sauropoda: Titanosauriformes) from the Upper Cretaceous of China. PloS ONE, 8(8): e69375.

Mocho P, Royo-Torres R, Malafaia E, Escaso E, Ortega F. in press. Turiasauria-like teeth from the Upper Jurassic of the Lusitanian Basin, Portugal, Historical Biology, 10.1080/08912963.2015.1049948

Table S.20. SI values table: values used for figure 8 on Mocho et al. (in press)

SUPPLEMENTARY MATERIAL 9

Measurements of Baleal, Paimogo, Praia de Areia Branca and Praia da Corva vertebrae

Measurement	SHN 530	MNHN.UL	MMPM/P-73	SHN 180
centrum anteroposterior width with the posterior condyle	15,1	16,8	17,3	13,9
centrum anteroposterior width	12,5	14,4	15	10,8
mediolateral width of the anterior articulation	28,6	34	27	22,5
dorsoventral width of the anterior articulation	31	34,5	27,2	21,2
mediolateral width of the posterior articulation	24	33,1	29,4	20,7
dorsoventral width of the posterior articulation	27,1	28	28,1	19,2
vertebra total height	?	?	?	41,8
anteroposterior width of the neural spine	?	?	?	7,73
transverse width of the neural spine on the apex	?	?	?	3,45

measurements in centimeters.

Table S.21. Measurements of Baleal, Paimogo, Praia de Areia Branca and Praia da Corva vertebrae

SUPPLEMENTARY MATERIAL 10

Measurements of *Lourinhasaurus alenquerensis*

Measurement	MG5780 (left)	MG30371 (right)
total length	1660	/
acromion process dorsoventral width	1075	1040
acromion ridge length	620	/
scapular blade length	990	/
dorsoventral width of scapular blade on its base	239	210
mediolateral width of scapular blade on its base	/	90
distal scapular blade width	510	/
maximum lateromedial width on acromion process	/	260

Table S.22. Measurements of *Lourinhasaurus alenquerensis* (scapulae)

Measurements	MG5780 (left)	MG30372 (right)
dorsoventral width	/	/
craniocaudal width	500	544
maximum lateromedial width on glenoid	/	264
cof maximum diameter	80	/
cof minimum diameter	43	/

Table S.23. Measurements of *Lourinhasaurus alenquerensis* (coracoids)

Measurements	MG2 (left)	MG4975 (right)
total length	1390	/
mediolateral length of proximal section	545	/
proximal craniocaudal width on humeral head	230	285
proximal craniocaudal width on lateral corner of proximal section	145	/
distal mediolateral width	450	/
distal craniocaudal width	295	/
minimum shaft mediolateral width	204	/
minimum shaft craniocaudal width	150	/
deltopectoral crest proximodistal width	620	/
deltopectoral crest mediolateral width	65	/

Table S.24. Measurements of *Lourinhasaurus alenquerensis* (humeri)

Measurements	MG4979 (left)
total length	1060
proximal craniocaudal width on olecranon	244
craniomedial process maximum width	395
craniolateral process maximum width	310
distal mediolateral width	207
distal craniocaudal width	160
minimum shaft mediolateral width	165
minimum shaft craniocaudal width	110
distal triangular suture proximodistal width	144
maximum distal triangular suture transversal width	117

Table S.25. Measurements of *Lourinhasaurus alenquerensis* (ulna)

Measurements	MG4979 (left)
total length	1010
proximal mediolateral width	252
proximal craniocaudal width	190*
minimum shaft mediolateral width	169
minimum shaft craniocaudal width	135
distal mediolateral width	216
distal craniocaudal width	180
**approximation*	

Table S.26. Measurements of *Lourinhasaurus alenquerensis* (radius)

Measurements	MG5781 (left)
craniocaudal width of ilium	1415
dorsoventral width on pubic peduncle and perpendicular to the craniodorsal width of the ilium	840
dorsoventral height of pubic peduncle	550
length from the most caudal point in the pubic peduncle to ischiatic peduncle	510
mediolateral width of pubic peduncle	318
craniocaudal width of pubic peduncle	215
mediolateral width of ischiatic peduncle	/
craniocaudal width of ischiatic peduncle	/
length from ischiatic peduncle to pos	400

Table S.27. Measurements of *Lourinhasaurus alenquerensis* (ilium)

Measurements	MG4970 (left)	MG4975 (right)
length from the most cranial point in the iliac peduncle to distal end	1130	980
craniocaudal width of proximal plate	385	/
length from the most caudal point in the iliac peduncle to distal end	1110	996
length from the most dorsal point in the ischiatic peduncle to distal end	966	/
pubic blade minimum craniocaudal width	200	/
iliac peduncle mediolateral width	280	245
iliac peduncle craniocaudal width	301	365
ischiatic peduncle mediolateral width	105-to-?*	/
ischiatic peduncle dorsoventral width	/	/
obturator foramen maximum diameter	95	/
obturator foramen minimum diameter	35	/
acetabulum length	275	/
craniocaudal width of the distal end	411	464
mediolateral width of the distal end	271	292
triangular suture dorsoventral width	245	/
triangular suture maximum mediolateral width	185	/
**(cranial-to-caudal)*		

Table S.28. Measurements of *Lourinhasaurus alenquerensis* (pubis)

Measurements	MG4957 (right)	MG4957 (left)
length from the most caudal point in the iliac peduncle to distal end	92	86
length from the most dorsal point in the pubic peduncle to distal end	1050	1070
length from the most ventral point in the pubic peduncle to distal end	92,5*	90
iliac peduncle mediolateral width	120	155
iliac peduncle craniocaudal width	240	210
pubic peduncle mediolateral width	/	105-to-46*
pubic peduncle dorsoventral width	/	425
maximum width of the distal end	167	170
width of the distal end perpendicular to the maximum width of distal end	92	85
distal symphysis maximum length	130	190
acetabulum length	/	265
craniocaudal width of proximal plate	29	28,5
length of most cranial point in iliac peduncle to most ventral point of pubic peduncle	55**	61,5
length of most caudal point in iliac peduncle to most ventral point of pubic peduncle	61**	64,7
length of most caudal point in iliac peduncle to most dorsal point in pubic peduncle	39	37,5
**(cranial-to-caudal)*		

Table S.29. Measurements of *Lourinhasaurus alenquerensis* (ischia)

Measurement	MG4931 (left)
total length	1680
proximal mediolateral width	580
proximal craniocaudal width on femoral head	285*
proximal craniocaudal width greater trochanter	270
distal mediolateral width	535
maximum width of tibial condyle	399
maximum width of tibial condyle	331
distal craniocaudal width on intecondylar	214
minimum shaft mediolateral width	310
minimum shaft craniocaudal width	180
4th trochanter proximodistal width	280
4th trochanter mediolateral width	90
4th trochanter height (from posterior face of the diaphysis)	45
**the cranial face of femoral head is eroded*	

Table S.30. Measurements of *Lourinhasaurus alenquerensis* (femur)

Measurement	MG4983 (left)
total length	1090
proximal mediolateral width	380
proximal craniocaudal width	360
distal mediolateral width	350
maximum width of pvp	258
maximum width of aspa	190
shaft minimum mediolateral width	127
shaft minimum craniocaudal width	205
cnemial crest length	440
cnemial crest deep	120

Table S.31. Measurements of *Lourinhasaurus alenquerensis* (tibia)

Measurement	MG4984 (left)
total length	1085
proximal mediolateral width	112
proximal craniocaudal width	202
distal mediolateral width	141
distal craniocaudal width	196
shaft minimum mediolateral width	125
shaft minimum craniocaudal width	85
lateral trochanter proximodistal width	200
lateral trochanter craniocaudal width	37
cranial trochanter proximodistal width	/
tibial suture proximodistal width	/
maximum tibial suture craniocaudal width	/

Table S.32. Measurements of *Lourinhasaurus alenquerensis* (fibula)

Measurements	MG30375 (left)
maximum craniocaudal width	24,5
maximum mediolateral width	/
minimum craniocaudal width	/
height on ascending process of astragalus	19
maximum diameter of fibula articular surface	12
minimum diameter of fibula articular surface	8

Table S.33. Measurements of *Lourinhasaurus alenquerensis* (astragalus)

Measurements	MG30378	MG4956										
	DV1	DV2	DV3	DV4	DV5	DV6	DV7	DV8	DV9	DV10	DV11	DV12
craniocaudal width	/	329	/	330	342	328	360	/	/	333	255	/
dorsoventral width on cranial face	/	154	243	236	231	325	196	177	186	337	343	338
mediolateral width on cranial face	/	282	336	342	354	/	354	374	364	/	347	266
dorsoventral width on caudal face	/	251	228	254	262	/	211	197	/	388	325	355
mediolateral width on caudal face	/	346	371	381	378	/	403	348	/	298	400	/
minimum mediolateral width of the centrum	/	162	209	247	242	/	229	225	214	171	266	205
right pleurocoelus craniocaudal width	/	/	87	115	103	/	90	/	/	79	85	74
right pleurocoelus dorsoventral width	/	/	/	/	/	/	52	/	/	82	/	/
left pleurocoelus craniocaudal width	/	111	115	/	116	/	/	94	/	103	93	75
left pleurocoelus dorsoventral width	/	/	/	/	/	/	/	/	/	85	/	/
elongation Index (EI)	/	0,95	/	0,87	0,90	/	0,89	/	/	1,12	0,64	/
craniocaudal width/Dorsoventral width on posterior face	/	1,31	/	1,30	1,31	/	1,71	/	/	0,86	0,78	/

Table S.34. Measurements of *Lourinhasaurus alenquerensis* (dorsal vertebrae)

Measurements	MG4956				
	1st Sacral	2nd Sacral	3rd Sacral	4th Sacral	5th Sacral
craniocaudal width	225	210	/	200	/
dorsoventral width on cranial face	332	/	/	/	/
mediolateral width on cranial face	325	/	/	/	/
dorsoventral width on caudal face	/	/	/	/	/
mediolateral width on caudal face	275	/	/	/	/
minimum mediolateral width of the centrum	248	/	/	/	/
right pleurocoelus craniocaudal width	/	-	-	-	-
right pleurocoelus dorsoventral width	/	-	-	-	-
left pleurocoelus craniocaudal width	50	-	-	-	-
left pleurocoelus dorsoventral width	42	-	-	-	-
elongation Index (EI)	0,82	/	/	/	/
craniocaudal width/Dorsoventral width on posterior face	/	/	/	/	/
- *ausente*					

Table S.35. Measurements of *Lourinhasaurus alenquerensis* (sacral vertebrae)

Measurement	**MG 4956**		
	most proximal to distal proximal caudal centra preserved		
craniocaudal width	180	182	170
dorsoventral width on cranial face	306	301	/
mediolateral width on cranial face	328	335	/
dorsoventral width on caudal face	318	276	237
mediolateral width on caudal face	305	315	/
minimum mediolateral width of the centrum	270	/	/
elongation Index (EI)	0,59	0,58	/
craniocaudal width/Dorsoventral width on posterior face	0,57	0,66	0,72
neural arch craniocaudal width on the base	115	115	99
neural arch height	150	/	/
right transverse process mediolateral width	/	26	/
left transverse process mediolateral width	35	/	/

Table S.36. Measurements of *Lourinhasaurus alenquerensis* (caudal proximal vertebrae)

SUPPLEMENTARY MATERIAL 11

Map of synapomorphies of Chapter 10 phylogenetic approach

Synapomorphies for nodes of phylogenetic hypothesis from Wilson (2002) data matrix

Node 1. Sauropoda. 108 (0→1), 127 (0→1), 149 (0→1), 160 (0→1), 165 (0→1), 166 (9→1), 167 (0→1), 169 (0→1), 172 (0→1), 185 (0→1), 192 (0→1), 194 (0→1), 196 (0→1), 198 (0→1), 211 (0→1), 216 (0→1), 222 (0→1), 225 (0→1), 230 (0→1); 231 (0→1).

Node 2, Eusauropoda. 190 (0→1), 197 (0→1), 204 (0→1), 208 (0→1), 217 (0→1), 221 (0→1), 223 (0→1), 226 (0→1), 227 (0→1), 229 (0→1), 232 (0→1); 233 (0→1).

Node 3. 81 (1→0), 94 (0→1), 96 (0→1), 99 (0→1), 100 (0→1), 101 (0→1); 109 (0→1), 150 (0→1).

Node 4. 78 (0→1), 83 (9→1), 108 (1→2).

Node 5. 218 (0→1).

Node 6. 80 (3→4), 86 (0→1), 87 (1→0), 118 (0→1).

Node 7. 58 (0→1), 98 (0→1), 102 (0→1), 145 (0→1), 175 (0→1), 210(0→1).

Node 8, Turiasauria. 161 (0→1), 163 (0→1), 164 (1→0).

Node 9. 83 (1→0).

Node 10, Neosauropoda. 4 (0→1), 51 (0→1), 123 (0→1), 124 (0→1), 154 (0→1), 195 (0→1), 203 (0→1), 212 (0→1).

Node 11. Diplodocoidea. 140 (0→1).

Node 12. 102 (1→0), 126 (0→1).

Node 13, Rebbachisauridae. 10 (1→1), 17 (0→1), 18 (1→9), 20 (1→0), 25 (0→1), 26 (1→9), 27 (0→9), 28 (1→9), 76 (0→2), 152 (0→2), 162 (1→0).

Node 14, Flagellicaudata. 5 (0→1), 56 (0→1), 73 (0→1), 85 (0→1), 89 (0→1), 90 (9→1); 95 (0→1), 121 (0→1), 128 (0→1), 145 (1→0), 189 (0→1), 194 (1→0), 195 (1→0), 220 (0→1).

Node 15, Dicraeosauridae. 19 (0→1), 23 (0→1), 27 (0→1), 45 (0→1), 47 (0→1), 49 (0→1).

Node 16, Diplodocidae. 14 (0→1), 15 (0→1), 80 (3→4), 88 (0→1), 122 (0→1), 129 (0→1), 130 (0→1).

Node 17. 86 (0→1), 118 (0→1), 119 (0→1), 120 (0→1), 131 (0→1), 132 (0→1), 133 (0→1).

Node 18, Macronaria. 59 (0→1), 73 (0→1), 105 (0→1), 142 (0→1), 177 (0→1), 178 (0→1), 190 (0→1).

Node 19, Camarasauridae. 98 (1→0), 126 (0→1).

Node 20, Titanosauriformes. 50 (0→1), 69 (1→0), 77 (0→1), 86 (0→1), 141 (0→1), 146 (0→1), 179 (0→1), 180 (0→1), 188 (0→1), 199 (0→1).

Node 21, Somphospondyli. 48 (0→1), 100 (1→0), 153 (0→1), 158 (0→1), 167 (1→0), 213 (1→0).

Node 22. 98 (1→0), 123 (1→0), 126 (0→1), 129 (0→1), 153 (1→0).

Node 23, Titanosauria. 81 (0→1), 83 (1→0), 98 (1→0), 104 (0→1), 106 (0→1), 118 (0→1), 132 (0→1), 193 (0→1), 205 (0→1), 234 (0→1).

Node 24. 134 (0→1), 155 (0→1), 163 (0→1), 164 (1→0), 170 (0→1).

Node 25. 22 (0→1).

Node 26, Saltasauridae. 86 (1→0), 156 (0→1), 157 (0→1), 168 (0→1), 171 (0→1), 187 (0→1), 201 (0→1).

Node 27. 81 (1→0), 135 (0→1).

Node 28. 117 (0→1), 148 (0→1), 233 (1→0).

Note: This map of synapomorphies was obtained from the topology of strict consensus.

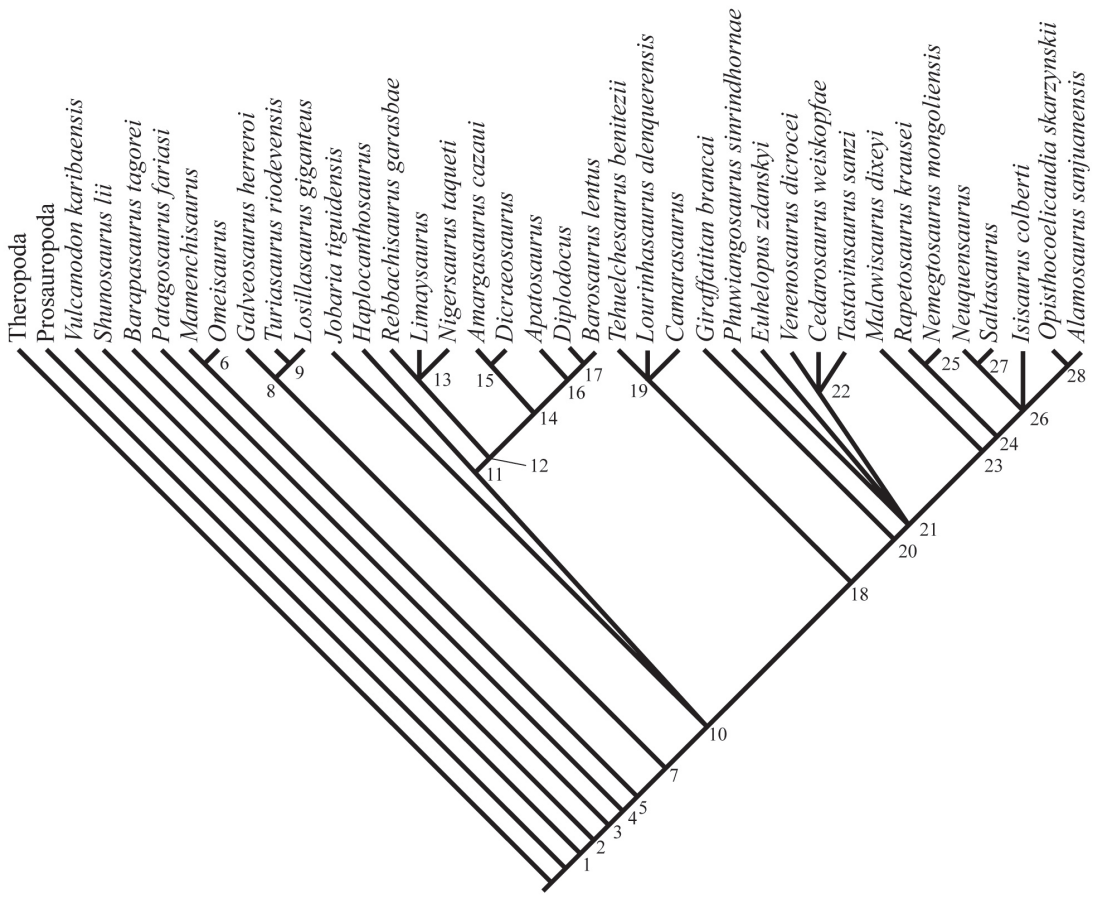

Figure S.1. Phylogenetic hypothesis based on Wilson (2002) data matrix with internal nodes numbered for list of synapomorphies

Synapomorphies for nodes of phylogenetic hypothesis from Upchurch et al. (2004) data matrix

Node 1, Sauropoda. 115 (0→1), 161 (0→1), 177 (0→1), 187 (0→1), 214 (0→1), 219 (0→1); 223 (0→1); 226 (0→1), 234 (0→1), 236 (0→1), 251 (0→1), 260 (0→1), 261 (0→1), 264 (0→1), 266 (0→1), 267 (0→1), 270 (0→1), 273 (0→1), 275 (0→1), 286 (0→1), 289 (0→1), 290 (0→1), 296 (0→1), 298 (0→1).

Node 2. 263 (0→1), 269 (0→1), 279 (0→1), 287 (0→1).

Node 3, Eusauropoda. 108 (0→1), 112 (0→1), 116 (0→1), 207 (0→1), 224 (1→0), 247 (0→1), 248 (0→1), 252 (0→1), 262 (0→1), 268 (1→0), 278 (0→1), 292 (0→1), 302 (0→1), 304 (0→1).

Node 4. 19 (0→1), 40 (0→1), 91 (0→1), 121 (0→1), 123 (0→1), 147 (0→1), 156 (0→1), 157 (0→1), 169 (0→1), 200 (0→1), 228 (0→1), 297 (0→1), 306 (0→1).

Node 5. 15 (0→1), 83 (0→1), 109 (0→1), 206 (0→1).

Node 6. 106 (0→1), 249 (0→1), 268 (0→1).

Node 7. 153 (0→1), 210 (0→2); 242 (0→1), 258 (0→1), 271 (0→1).

Node 8. 82 (1→0), 131 (0→1), 253 (0→1), 295 (1→0).

Node 9. 110 (1→2).

Node 10. 67 (0→1), 150 (0→1).

Node 11, Turiasauria. 154 (0→1), 201 (1→0), 219 (1→0), 222 (0→1).

Node 12, Neosauropoda. 20 (0→1), 110 (1→2), 135 (0→1), 144 (1→0), 202 (0→1), 239 (0→1), 274 (0→1), 276 (0→1), 283 (0→1).

Node 13, Diplodocoidea. 1 (1→2), 3 (0→1), 7 (0→1), 12 (0→1), 13 (0→1), 14 (0→1), 19 (1→0), 41 (0→1), 85 (1→0), 88 (0→1), 95 (0→1).

Node 14. 26 (0→1), 44 (0→1), 48 (0→1), 71 (0→1), 73 (1→0).

Node 15. 50 (0→1), 51 (0→1), 53 (0→1), 68 (0→1), 89 (0→1).

Node 16, Flagellicaudata. 47 (0→1), 66 (1→0), 67 (1→0), 118 (0→2), 173 (0→1), 191 (0→1), 195 (1→0), 257 (0→1), 258 (1→0), 293 (0→1).

Node 17, Dicraeosauridae. 36 (0→1), 43 (0→1), 49 (0→1), 54 (0→1), 55 (0→1), 110 (2→0), 128 (1→0), 129 (1→0).

Node 18, Diplodocidae. 46 (0→1), 56 (0→1), 84 (1→0), 98 (0→1), 102 (0→1), 125 (0→1), 138 (1→0), 178 (0→1).

Node 19. 114 (0→1), 146 (0→1), 181 (0→1), 182 (0→1), 183 (0→1).

Node 20, Macronaria. 127 (0→1), 159 (0→1), 199 (1→0).

Node 21, Camarasauromorpha. 105 (0→1), 142 (0→1), 253 (0→1).

Node 22, Camarasauridae. 137 (1→0), 138 (1→0), 210 (2→0).

Node 23, Titanosauriformes. 131 (0→1), 160 (0→1), 185 (0→1), 240 (0→1), 244 (0→1), 245 (0→1), 309 (0→1).

Node 24. 152 (0→1), 184 (0→1), 216 (0→1), 219 (1→0), 293 (0→1).

Node 25. 137 (1→0), 186 (0→1).

Node 26. 183 (0→1), 211 (0→1), 225 (0→1), 277 (1→0).

Node 27, Somphospondyli. 110 (2→0), 148 (0→2), 149 (0→1), 256 (0→1), 272 (0→1).

Node 28, Titanosauria. 221 (0→1), 222 (0→1).

Node 29, Lithostrotia. 173 (0→1), 174 (0→1), 177 (1→0), 186 (0→1).

Node 30. 84 (1→0), 175 (0→1), 184 (0→1).

Node 31. 171 (0→1).

Node 32. 130 (0→1), 182 (0→1).

Node 33. 131 (1→0), 153 (1→0).

Node 34. 184 (1→0).

Node 35. Saltasauridae. 189 (0→1), 217 (0→1).

Note: This map of synapomorphies was obtained from the topology of strict consensus.

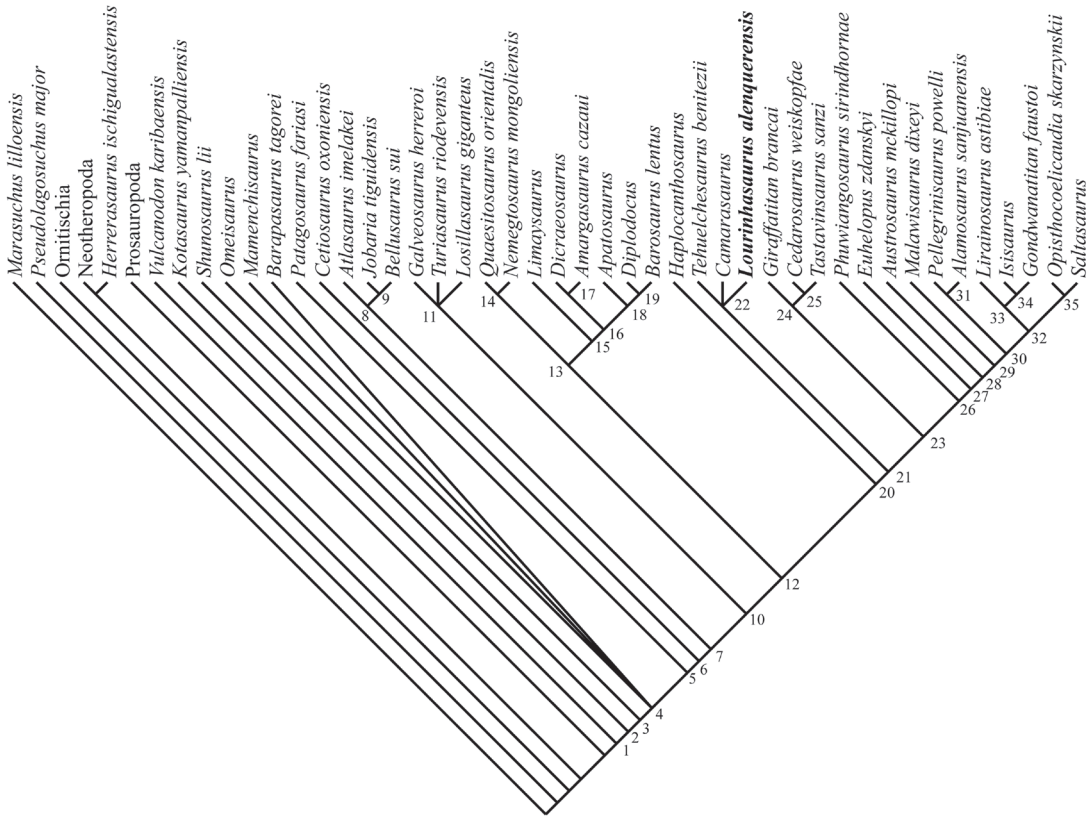

Figure S.2. Phylogenetic hypothesis based on Upchurch *et al*. (2004) data matrix with internal nodes numbered for list of synapomorphies.

References

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SUPPLEMENTARY MATERIAL 12

Data matrix information for Chapter 10 phylogenetic approach

Changes in Wilson (2002) and Upchurch et al. (2004) data matrix

Wilson (2002) data matrix

- *Brachiosaurus → Giraffatitan brancai*: 146 (0→1), 198 (1→2).

In character #98 and #101, the Wilson (2002) codification was maintained. In figured material of *Giraffatitan* (Janensch, 1950, p. 49) is possible to test the presence of a pcpl in middle and caudal centra (character #98) and the presence of the contact between spol and spdl in the middle and caudal dorsal neural spines (character #101). Taylor (2009) and Wilson (2002) considered that Giraffatitan chevrons have short haemal channel, i.e., the plesiomorphic state [0] for character #146 of Wilson (2002) data matrix. Nevertheless, the chevrons figured by Janensch 1950, the haemal channel surpass significantly the 25% of total chevron total length, 41-46 % sensu Royo-Torres (2009). For #200 it was accepted the Wilson (2002) codification, a tibial condyle larger than fibular condyle (Janensch, 1961).

- *Cedarosaurus weiskopfae*: 77, 78 (?→1); 106 (?→0); 141 (0→?); 142, 154 (?→1); 158 (?→0); 164 (0→1); 166 (?→1); 171 (1→0); 175, 177 (?→1); 192, 193, 234 (?→0).
- *Venenosaurus dicrocei*: 78, 114 (?→1); 118 (1→0); 145, 146 (?→1); 153 (?→0); 154, 175 (?→1); 192, 193 (? →0).

Upchurch et al. (2004) data matrix

- *Brachiosaurus → Giraffatitan brancai*: 124 (?→0); 135 (1→0); 141 (?→0); 152, 157 (0→1); 172 (1→0&1); 184, 196 (0→1); 208 (1→0) based on Janensch (1936, 1950, 1961) and Taylor (2009).

The dorsal vertebrae of *Giraffatitan* bears two different states for dorsal centra ventral face (Janensch, 1950): i) a transverse concave ventral face bordered by ventrolateral keels (15th to 17th presacral vertebrae) and ii) a ventral face with a medial keel in remain dorsal centra. Herein, it is followed the codification of Upchurch et al. (2004, character #126[0&2]) contra Taylor (2009) codification (character #134[1, rounded ventral face]). Taylor (2009) considered the caudal margins of crania dorsal pleurocoels as rounded, but, it also was maintained the Upchurch et al. (2004) codification for #127, option followed in more recent works (e.g. Mannion et al. 2013). Taylor suggested that proximal caudal centra are subcircular, but, in Janensch (1950) it is possible to observe a transition along the proximal centra between subcircular and dorsoventrally compressed centra. Taking into account this condition, we decided to quote #172 of Upchurch et al. (2004) data matrix as 0&1. In #208 the apomorphic state is assumed (as Upchurch et al., 2004) due Giraffatitan coracoids subquadrangular format. For #271 it was accepted the Upchurch et al. (2004) codification, a tibial condyle larger than fibular condyle (see Janensch 1961).

- *Camarasaurus*: 142 (0→1), it is present in some *Camarasaurus grandis* caudal dorsal vertebrae (Ostrom & McIntosh, 1966, p.114).
- *Cedarosaurus weiskopfae*: 142 (0→1); 145 (?→0); 309 (?→1) (based on R. Royo-Torres, pers. observ, 20.. ; based on D'Emic, (2012a) and D'Emic (2012b).
- *Tastavinsaurus sanzi*: 105 (?→1), 142 (0→1), 151 (1→0), 249 (0→1).
- *Tehuelchesaurus benitezii*: 105 (?→1); 126, 127 (?→1); 129 (0→1); 131 (?→0); 132, 136 (?→1); 137 (?→0); 138, (1→0); 139 (?→0); 142 ,143 (?→1); 145 (?→0); 146 (?→1); 148, 149, 150, 151, 152, 153, 154, 155 (?→0); 156, 157 (?→1); 158, 160 (?→0); 161 (?→1); 165, 201 (0→1); 202 (?→1); 208, 253 (0→1); 257 (1→0); 258 (?→1); 262 (?→1); 266 (?→1); 267 (0→1); 268 (?→1); 272, 309 (?→0); based on Carballido et al. (2011).

Lourinhasaurus alenquerensis codification for Wilson (2002) data matrix

????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?01?? 011?? 0??1? ?1?1? 110?? ?1??1 ??2?? ?10?? ??00? 00100 1100? 00??? ????? 01??? ???11 01010 00001 01011 11010 01?1? ????? ????1 10001 ?1011 11101 00110 1?101 1?10? ????? ????? ????? ???0

Lourinhasaurus alenquerensis codification for Upchurch et al. (2004) data matrix

????? ?0111 11??2 ????1 1???? ???00 01110 0?1?1 10??? ????? ?1?0? ??1?? ????0 110?1 001?? ?000? ?1??? 010?? ?1001 ?0?1? ????1 110?? 111?0 00011 00010 00100 11??0 ????? ????? ?1000 11110 11?00 00101 11110 11111 10111 111?1 01?11 11??? ????? ????? ????? ???0

Alterations in Upchurch et al. (2004) data matrix by Upchurch and Mannion (2009)

- *Nemegtosaurus mongoliensis*: 45 (?→0).
- *Omeisaurus*: 277 (?→1).
- *Opisthocoelicaudia skarzynskii*: 277 (?→0).
- *Limaysaurus*: 277 (?→1);
- *Saltasaurus*: 277 (?→0);
- *Shunosaurus lii*: 277 (?→1);
- *Vulcanodon karibaensis*: 277 (? →0);
- Ornithischia: 60 (?→0), 160 (p →0);
- *Andesaurus delgadoi*: 173 (0→1);
- *Alamosaurus sanjuanensis*: 266 (? →1).

Tehuelchesaurus benitezii codification for Wilson (2002) data matrix

????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?01?? ????? ????? ?001? 10010 10101 00?1? ????? ????? ????? ????? ????? ????? 01??? ???11 00010 01?01 01011 11010 0???? ????? ????1 ???01 11011 11100 00??? ????? ????? ????? ????? ????? ????

Constrained analyses

- Initial constrain for outgroup topology in Upchurch *et al*. (2004): force = (1 (2 ((3 4) (5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45)))).
- *Lourinhasaurus* as a non-neosauropod in Wilson (2002) data matrix: force = (8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 32 33 34 35 37).
- *Lourinhasaurus* more derived than Camarasauridae in Wilson (2002) data matrix: force = (10 16 18 22 23 24 25 26 27 28 32 33 34 35 36).
- *Lourinhasaurus* more primitive than Macronaria (*Camarasaurus*) in Wilson (2002) data matrix: force = (10 16 18 12 22 23 24 25 26 27 28 32 33 34 35 37).

- *Tehuelchesaurus* more derived than Camarasauridae in Wilson (2002) data matrix: force = (10 16 18 22 23 24 25 26 27 28 32 33 34 35 37).
- *Lourinhasaurus* as non-neosauropod in Upchurch et al. (2004) data matrix: force = (1 (2 ((3 4) (5 9 11 13 17 23 24 26 28 30 32 38 41 42 43 44 (7 8 6 10 12 14 15 16 18 19 20 21 22 25 27 29 31 33 36 34 35 37 39 40 45))))).
- *Lourinhasaurus* more derived than Camarasauridae in Upchurch et al. (2004) data matrix: force = (1 (2 ((3 4) (5 7 8 9 11 12 13 15 17 18 19 22 23 24 28 29 30 32 35 36 38 39 40 41 42 43 44 (6 10 14 16 20 21 25 26 27 31 33 34 37 45))))).
- *Lourinhasaurus* more primitive than Macronaria (*Haplocanthosaurus*) in Upchurch et al. (2004): force = (1 (2 ((3 4) (5 7 8 9 11 12 13 17 18 19 23 24 26 28 29 30 32 35 36 38 41 42 43 44 (6 10 14 15 16 20 21 22 25 27 31 33 34 37 39 40 45))))).
- *Tehuelchesaurus* more derived than Camarasauridae in Upchurch et al. (2004): force = (1 (2 ((3 4) (5 7 8 9 11 12 13 15 17 18 19 22 23 24 26 28 29 30 32 35 36 38 41 42 43 44 (6 10 14 16 20 21 25 27 31 33 34 37 39 40 45))))).

References

Carballido JL, Rauhut OWM, Pol D, Salgado L. 2011. Osteology and phylogeny relationships of *Tehuelchesaurus benitezii* (Dinosauria, Sauropoda) from the Upper Jurassic of Patagonia. Zoological Journal of the Linnean Society, 163: 605-662.

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Wilson JA. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. Zoological Journal of the Linnean Society, 136: 217-276.

SUPPLEMENTARY MATERIAL 13

Bootstrap values for Chapter 10 phylogenetic approach

Bootstrap values for the phylogenetic hypothesis obtaining using Wilson (2002) data matrix

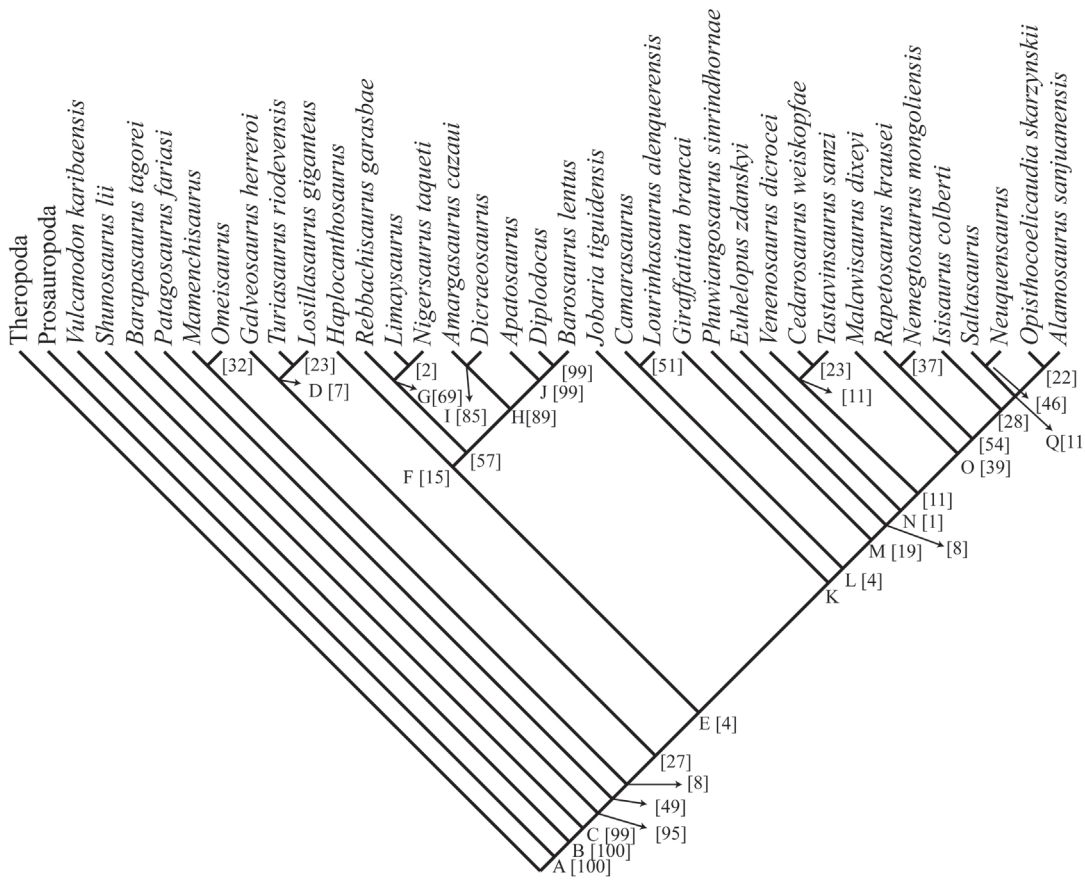

Figure S.3. MPT of 509 steps with a consistency index (CI) of 0.562 and a retention index (RI) of 0.754 obtained from Wilson (2002) data matrix. The numbers are percentage value support in bootstrap analysis with 10000 replicates; absence number means support is <50%; A – Sauropodomorpha, B – Sauropoda, C – Eusauropoda, D – Turiasauria, E – Neosauropoda, F – Diplodocoidea, G – Rebbachisauridae, H – Flagellicaudata, I – Dicraeosauridae, J- Diplodocidae, K – Macronaria, L – Camarasauromorpha, M – Titanosauriforme, N – Somphospondyli, O – Titanosauria, P- Lithostrotia, Q – Saltasauridae.

Bootstrap values for the phylogenetic hypothesis obtaining using Upchurch *et al.* (2004) data matrix

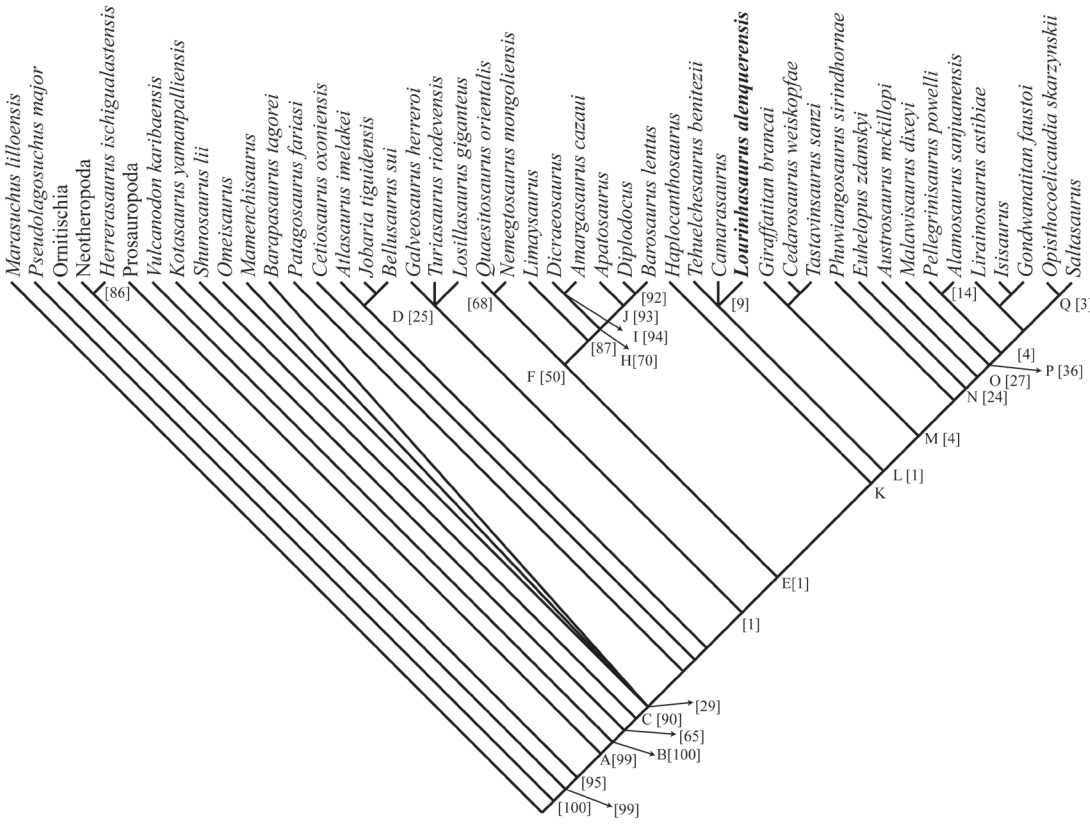

Figure S.4. Strict consensus of 18 MPTs of 678 steps with a consistency index (CI) of 0.473 and a retention index (RI) of 0.781 obtained from Upchurch et al. (2004) data matrix. The numbers are percentage value support in bootstrap analysis with 10000 replicates; absence number means support is <50%; A – Sauropodomorpha, B – Sauropoda, C – Eusauropoda, D – Turiasauria, E – Neosauropoda, F – Diplodocoidea, G – Rebbachisauridae, H – Flagellicaudata, I – Dicraeosauridae, J- Diplodocidae, K – Macronaria, L – Camarasauromorpha, M – Titanosauriforme, N – Somphospondyli, O – Titanosauria, P- Lithostrotia, Q – Saltasauridae.

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SUPPLEMENTARY MATERIAL 14

Measurements of *Lusotitan atalaiensis*

Measurement	MG2 (left)	MG4975 (right)
total length	/	/
mediolateral length of proximal section	590	540
anteroposterior width on humeral head	/	230
anteroposterior width on lateral corner of proximal section	/	125
distal mediolateral width	/	/
distal anteroposterior width	/	/
minimum shaft mediolateral width	/	225
minimum shaft anteroposterior width	/	145
deltopectoral crest dorsoventral width	/	400
deltopectoral crest mediolateral width	/	/

Table S.37. Measurements of *Lusotitan atalaiensis* (humeri)

Measurement	MG4979 (left)	MG4950 (right)
total length	1140	/
proximal mediolateral width	300	/
proximal anteroposterior width	175	/
minimum shaft mediolateral width	140	/
minimum shaft anteroposterior width	55	/
distal mediolateral width	257	250
distal anteroposterior width	152	185

Table S.38. Measurements of *Lusotitan atalaiensis* (radius)

Measurement	MG4966 (left)
total length	/
proximal anteroposterior width on olecranon	250
anteromedial process maximum width	/
anterolateral process maximum width	390
distal mediolateral width	/
distal anteroposterior width	/
minimum shaft mediolateral width	/
minimum shaft anteroposterior width	/
distal triangular suture dorsoventral width	/
maximum distal triangular suture transversal width	/

Table S.39. Measurements of *Lusotitan atalaiensis* (ulna)

Measurement	MG4952 (left)
length from the most anterior point in the iliac peduncle to distal end	600
anteroposterior width of proximal plate	336
length from the most posterior point in the iliac peduncle to distal end	760
length from the most dorsal point in the ischiatic peduncle to distal end	715
iliac peduncle mediolateral width	46
iliac peduncle anteroposterior width	183
ischiatic peduncle mediolateral width	269
ischiatic peduncle dorsoventral width	35-50*
acetabulum length	205
anteroposterior width of the distal end	427
mediolateral width of the distal end	180

Table S.40. Measurements of *Lusotitan atalaiensis* (pubis)

Measurement	MG4957 (left)
length from the most posterior point in the iliac peduncle to distal end	/
length from the most dorsal point in the pubic peduncle to distal end	/
length from the most ventral point in the pubic peduncle to distal end	/
iliac peduncle mediolateral width	150
iliac peduncle anteroposterior width	182
pubic peduncle mediolateral width	≈5
pubic peduncle dorsoventral width	315
maximum width of the distal end	/
width of the distal end perpendicular to the maximum width of distal end	/
distal symphysis maximum length	/
acetabulum length	210
anteroposterior width of proximal plate	254

Table S.41. Measurements of *Lusotitan atalaiensis* (ischium)

Measurement	MG4984 (left)
total lenght	/
proximal mediolateral width	105
proximal anteroposterior width	273
distal mediolateral width	/
distal anteroposterior width	/
shaft minimum mediolateral width	/
shaft minimum anteroposterior width	/
lateral trochanter dorsoventral width	/
lateral trochante anteroposterior width	/

Table S.42. Measurements of *Lusotitan atalaiensis* (fibula)

*The measurements for dorsal and caudal vertebrae, tibia and astragalus are present in Mannion *et al*., (2013)

Measurements in cm.

SUPPLEMENTARY MATERIAL 15

Map of synapomorphies of Chapter 11 phylogenetic approach

Synapomorphies for the nodes of phylogenetic hypothesis obtained from Wilson (2002) data matrix

Node 1. No synapomorphies.

Node 2. 108 (0→1), 127 (0→1), 149 (0→1), 160 (0→1), 165 (0→1), 166 (-→1), 167 (0→1), 169 (0→1), 172 (0→1), 185 (0→1), 192 (0→1), 194 (0→1), 196 (0→1), 198 (0→1), 211 (0→1), 216 (0→1), 222 (0→1), 225 (0→1), 230 (0→1), 231 (0→1).

Node 3. 190 (0→1), 197 (0→1), 204 (0→1), 208 (0→1), 217 (0→1), 221 (0→1), 223 (0→1), 226 (0→1), 227 (0→1), 232 (0→1), 233 (0→1).

Node 4. 81 (1→0), 94 (0→1), 96 (0→1), 99 (0→1), 100 (0→1), 101 (0→1), 109 (0→1), 150 (0→1).

Node 5. 78 (0→1), 83 (0→1), 108 (1→2), 137 (-→0).

Node 6, Mamenchisauridae. 72 (2→1), 80 (3→4), 84 (0→1), 86 (0→1), 87 (1→0), 118 (0→1).

Node 7, Turiasauria. 98 (0→1), 102 (0→1), 161 (0→1), 163 (0→1), 164 (1→0).

Node 8. 83 (1→0).

Node 9, Neosauropoda. 4 (0→1), 12 (0→1), 51 (0→1), 102 (0→1), 123 (0→1), 124 (0→1), 154 (0→1), 184 (0→1), 195 (0→1), 203 (0→1), 212 (0→1).

Node 10, Diplodocoidea. 1 (1→0), 2 (1→0), 22 (0→1), 46 (0→1), 53 (0→1), 65 (1→2), 66(1→2), 70(1→2), 74 (0→1), 102 (1→0), 126 (0→1), 137 (0→1), 140 (0→1).

Node 11, Rebbachisauridae. 10 (1→0), 17 (0→1), 18 (1→-), 20 (1→0), 25 (0→1), 26 (1→-), 27 (0→-), 28 (1→-), 76 (0→1), 152 (0→2), 162 (1→0).

Node 12, Flagellicaudata. 5 (0→1), 56 (0→1), 73 (0→1), 85 (0→1), 89 (0→1), 90 (- →1), 95 (0→1), 121 (0→1), 128 (0→1), 189 (0→1), 194 (1→0), 195 (1→0), 220 (0→1).

Node 13, Dicraeosauridae. 19 (0→1), 23 (0→1), 27 (0→1), 45 (0→1), 47 (0→1), 49 (0→1).

Node 14, Diplodocidae. 14 (0→1), 15 (0→1), 80 (3→4), 88 (0→1), 122 (0→1), 129 (0→1), 130 (0→1).

Node 15, Diplodocinae. 86 (0→1), 118 (0→1), 119 (0→1), 120 (0→1), 131 (0→1), 132 (0→1), 133 (0→1).

Node 16, Macronaria. 59 (0→1), 73 (0→), 77 (0→1), 86 (0→1), 89 (0→1), 105 (0→1), 126 (0→1), 141 (0→1), 142 (0→1), 143 (1→0), 146 (0→1), 177 (0→1), 178 (0→1), 179 (0→1), 180 (0→1), 188 (0→1), 191 (0→1), 199 (0→).

Node 17, Lithostrotia. 81 (0→1), 83 (1→0), 89 (1→0), 104 (0→1), 106 (0→1), 118 (0→1), 132 (0→1), 158 (0→1), 159 (0→1), 167 (1→0), 193 (0→1), 205 (0→1), 234 (0→1).

Node 18. 134 (0→), 155 (0→1), 163 (0→1), 164 (1→0), 170 (0→1).

Node 19, Nemegtosaurinae. 22 (0→1), 43 (0→1).

Node 20, Saltasauridae. 86 (1→0), 156 (0→1), 157 (0→1), 168 (0→1), 171 (0→1), 187 (0→1), 201 (0→1).

Node 21, Opisthocoelicaudinae. 117 (0→1), 148 (0→1), 234 (1→0).

Node 22, Saltasaurinae. 81 (1→0), 135 (0→1).

Note: This map of synapomorphies was obtained from the topology of consensus strictus.

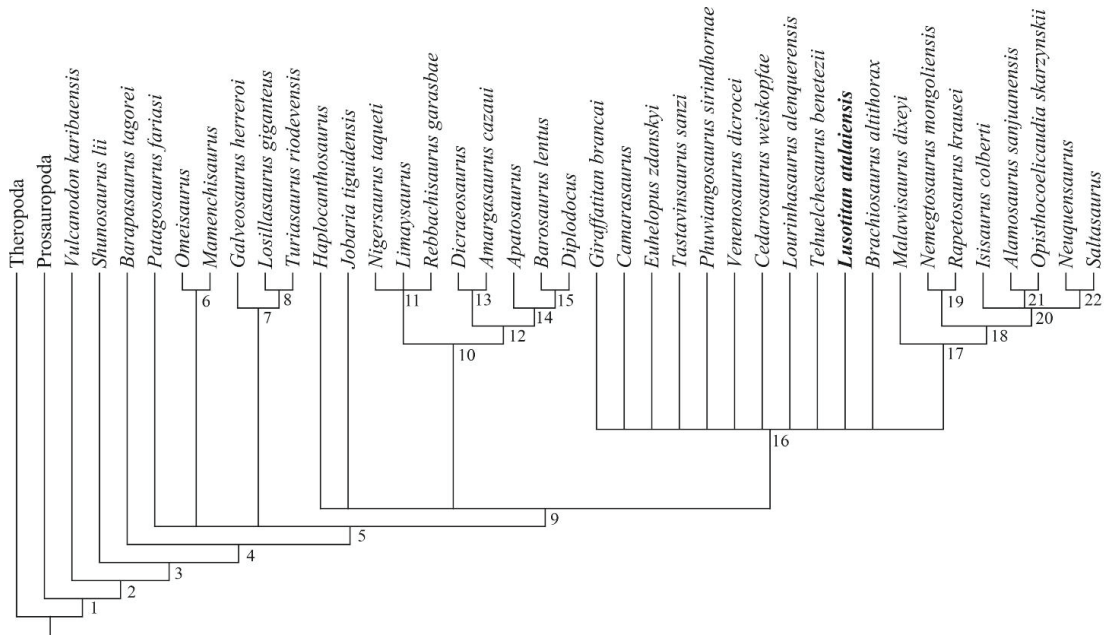


Figure S.5. Phylogenetic hypothesis based on Wilson (2002) data matrix with internal nodes numbered for list of synapomorphies.

Synapomorphies for the nodes of phylogenetic hypothesis obtained from Upchurch et al. (2004) data matrix

Node 1, Sauropoda. 115 (0→), 161 (0→1), 177 (0→1), 187 (0→1), 214 (0→1), 219 (0→1), 223 (0→1), 226 (0→1), 234 (0→1), 236 (0→1), 251 (0→1), 260 (0→1), 261 (0→1), 264 (0→1), 266 (0→1), 267 (0→1), 270 (0→1), 273 (0→1), 275 (0→1), 286 (0→1), 289 (0→1), 290 (0→1), 296 (0→1), 298 (0→1).

Node 2. 263 (0→1), 260 (0→1), 279 (0→1), 287 (0→1).

Node 3, Eusauropoda. 108 (0→1), 112 (0→1), 116 (0→1), 207 (0→1), 224(1→0), 247 (0→1), 248 (0→1), 252 (0→1), 262 (0→1), 268 (1→0), 278 (0→1), 292 (0→1), 302 (0→1), 304 (0→1).

Node 4. 19 (0→1), 40 (0→1), 91 (0→1), 121 (0→1), 123 (0→1), 147 (0→1), 156 (0→1), 157 (0→1), 169 (0→1), 200 (0→1), 228 (0→1), 297 (0→1), 306 (0→1).

Node 5. 15 (0→1), 83 (0→1), 109 (0→1), 206 (0→1).

Node 6. 106 (0→1), 249 (0→1), 268 (0→1).

Node 7. 153 (0→1), 210 (0→2), 242 (0→1), 258 (0→1), 271 (0→1).

Node 8. 82 (1→0), 131 (0→1), 253 (0→1), 295 (1→0).

Node 9. 110 (1→2).

Node 10. 67 (0→1), 150 (0→1).

Node 11, Turiasauria. 154 (0→1), 201 (1→0), 219 (1→0), 222 (0→1).

Node 12, Neosauropoda. 20 (0→1), 110 (1→2), 135 (0→1), 144 (1→0), 202 (0→1), 239 (0→1), 274 (0→1), 276 (0→1), 283 (0→1).

Node 13, Diplodocoidea. 1 (1→2), 3 (0→1), 7 (0→1), 12 (0→1), 13 (0→1), 14 (0→1), 19 (1→0), 41 (0→1), 85 (1→0), 88 (0→1), 95 (0→1).

Node 14, Nemegtosaurinae. 26 (0→1), 44 (0→1), 48 (0→1), 71 (0→1), 73 (1→0).

Node 15. 50 (0→1), 51 (0→1), 53 (0→1), 68 (0→1), 89 (0→1).

Node 16, Flagellicaudata. 47 (0→1), 66 (1→0), 67 (1→0), 118 (0→2), 173 (0→1), 191 (0→1), 195 (1→0), 257 (0→1), 258 (1→0), 293 (0→1).

Node 17, Dicraeosauridae. 36 (0→1), 43 (0→1), 49 (0→1), 54 (0→1), 55 (0→1), 110 (2→0), 128 (1→0), 129 (1→0).

Node 18, Diplodocidae. 46 (0→1), 56 (0→1), 84 (1→0), 98 (0→1), 102 (0→1), 125 (0→1), 138 (1→0), 178 (0→1).

Node 19, Diplodocinae. 114 (0→1), 146 (0→1), 181 (0→1), 182 (0→1), 183 (0→1).

Node 20, Macronaria. 127 (0→1), 159 (0→1), 199 (1→0).

Node 21, Camarasauromorpha. 105 (0→1), 142 (0→1), 253 (0→1).

Node 22, Camarasauridae. 137 (1→0), 138 (1→0), 210 (2→0).

Node 23, Titanosauriformes. 131 (0→1), 160 (0→1), 185 (0→1), 240 (0→1), 244 (0→1), 245 (0→1), 309 (0→1).

Node 24, Brachiosauridae. 152 (0→1), 184 (0→1), 216 (0→1), 219 (1→0), 293 (0→1).

Node 25. 138 (1→0), 142 (1→0), 154 (0→1).

Node 26. 253 (1→0).

Node 27. 186 (0→1).

Node 28, Somphospondyli. 183 (0→1), 211 (0→1), 225 (0→1), 277 (1→0).

Node 29. 110 (2→0), 148 (0→2), 149 (0→1), 218 (0→1), 256 (0→1), 272 (0→1).

Node 30. Titanosauria. 221 (0→1), 222 (0→1).

Node 31, Lithostrotia. 173 (0→1), 174 (0→1), 177 (1→0), 186 (0→1).

Node 32. 84 (1→0), 175 (0→1), 184 (0→1).

Node 33. 171 (0→1).

Node 34, Saltasauridae. 130 (0→1), 182 (0→2).

Node 35. 131 (1→0), 153 (1→0).

Node 36. 184 (1→0).

Node 37. 189 (0→1), 217 (0→1).

Note: This map of synapomorphies was obtained from the topology of consensus strictus.

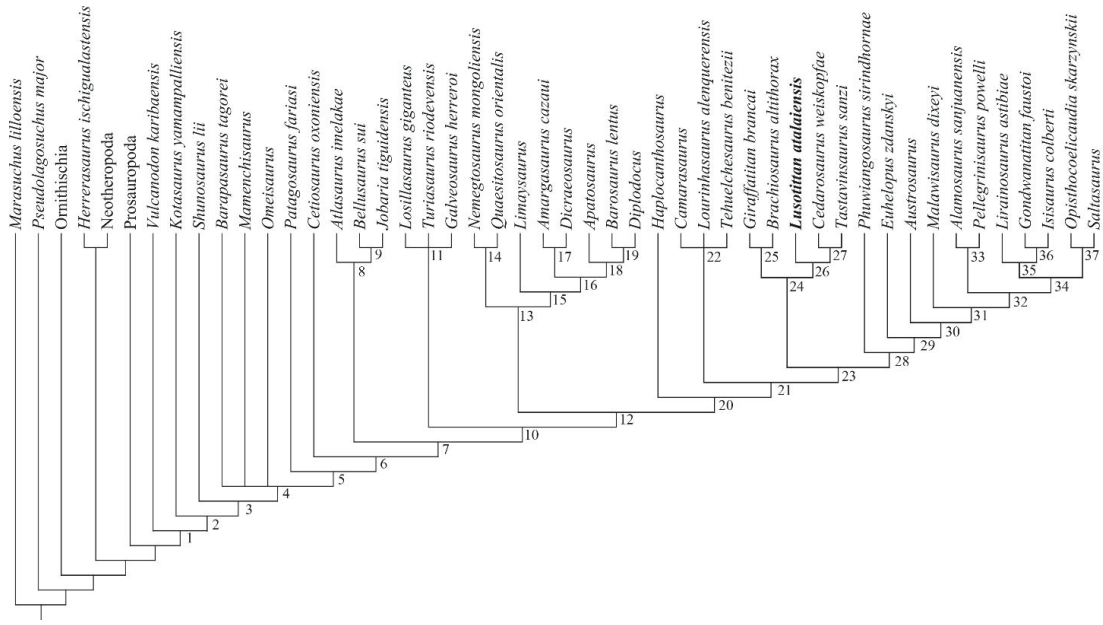


Figure S.6. Phylogenetic hypothesis based on Upchurch et al. (2004) data matrix with internal nodes numbered for list of synapomorphies.

Synapomorphies for the nodes of phylogenetic hypothesis obtained from D'Emic (2012) data matrix

Node 1. No synapomorphies.

Node 2. 71 (0→1), 95 (0→1).

Node 3. 88 (0→1).

Node 4, Neosauropoda. 5 (0→1).

Node 5, Macronaria. 11 (0→1), 12 (0→1), 39 (0→1), 41 (0→1), 79 (0→1), 89 (0→1).

Node 6. 43 (0→1), 64 (0→1), 107 (0→1).

Node 7, Titanosauriformes. 18 (0→1), 36 (0→1), 63 (0→1), 69 (0→1), 81 (0→1), 85 (0→1), 86 (0→1), 101 (0→1), 105 (0→1).

Node 8, Brachiosauridae. 5 (1→0), 9 (0→1), 15 (0→1), 40 (0→1), 105 (0→1).

Node 9. 2 (0→1), 3 (0→1).

Node 10. 79 (1→0).

Node 11, Somphospondyli. 18 (1→2), 34 (0→1), 68 (0→1), 109 (0→1).

Node 12. 70 (0→1), 111 (0→1), 114 (1→0).

Node 13. 37 (0→1), 113 (0→1).

Node 14. 47 (0→1), 50 (0→1), 116 (0→1).

Node 15, Euhelopodidae. 22 (0→1), 25 (0→1).

Node 16. 29 (0→1).

Node 17. 24 (0→1).

Node 18. 18 (2→0).

Node 19. 46 (0→1), 83 (0→1).

Node 20, Titanosauria. 54 (0→1), 103 (0→1).

Node 21, Lithostrotia. 45 (0→1), 48 (0→1), 53 (1→0), 55 (0→1), 104 (0→1).

Node 22, Saltasauridae. 42 (0→1), 52 (0→1), 57 (0→1), 74 (0→1), 80 (0→1), 82 (0→1), 87 (0→1).

Node 23. 61 (0→1), 62 (0→), 84 (0→1), 108 (0→1).

Note: This map of synapomorphies was obtained from the topology of consensus strictus.

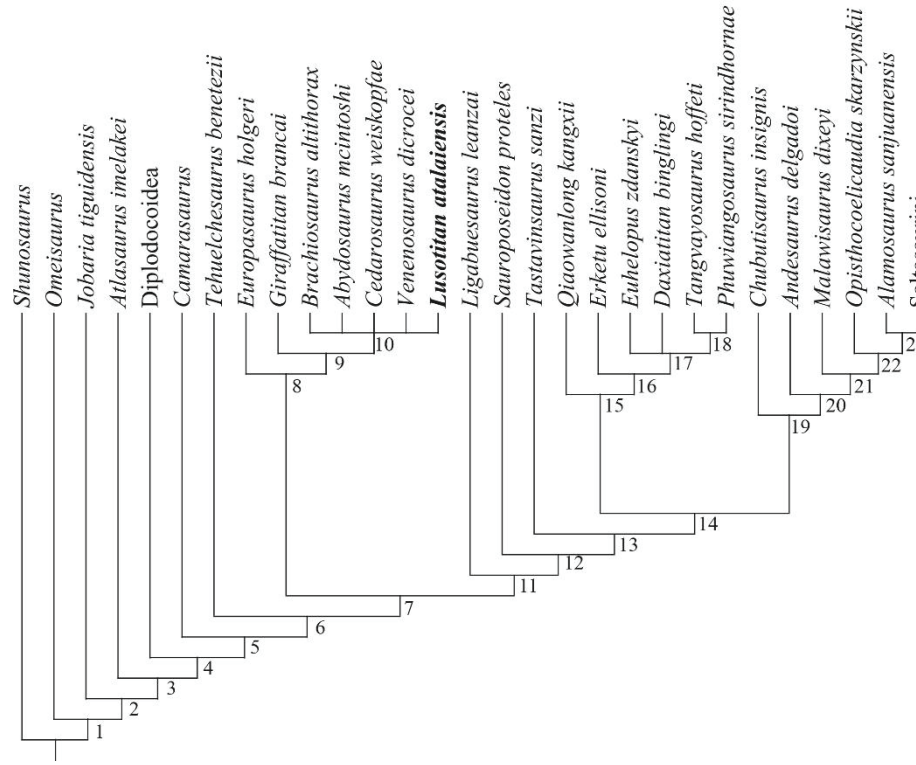


Figure S.7. Phylogenetic hypothesis based on D'Emic (2012) data matrix with internal nodes numbered for list of synapomorphies.

References

D'Emic MD. 2012. The early evolution of titanosauriform sauropod dinosaurs. Zoological Journal of the Linnean Society, 166(3): 624-671.

Wilson JA. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. Zoological Journal of the Linnean Society, 136: 217-276.

Upchurch P, Barrett PM, Dodson P. 2004. Sauropoda, p. 259-322. In: Weishampel DB, Dodson P, Osmólska H. (eds.), The Dinosauria II. University Of California Press, Berkeley.

SUPPLEMENTARY MATERIAL 16

Data matrix information for Chapter 11 phylogenetic approach

Changes in Wilson (2002), Upchurch et al. (2004) and D'Emic (2012) data matrices

Wilson (2002) data matrix

- *Tastavinsaurus sanzi*: 116 (1→2)*; 118 (1→0)*; 144 (0→9)*; 171 (1→0); 192 (1→0); 193 (1→0)*; 211 (?→1).
- *Turiasaurus*: 171 (1→0).
- *Venerosaurus*: 116 (?→2)*; 117(?→0)* 133 (0→1); 167 (0→1); 192 (0→1); 234 (?→0)*.
- *Cedarosaurus*: 116 (0→?)*, 117(0→?); 167 (0→1); 144 (?→9); 192 (0→1)
- *Galveosaurus*: 144 (?→9)

*Updates from Royo-Torres et al. (2014) data matrix.

Upchurch et al. (2004) data matrix

- *Giraffatitan brancai*: 218 (1→0).

D'Emic (2012) data matrix

- *Tastavinsaurus sanzi*: 18 (2→?); 36 (0→?); 56 (0→1); 60 (0→1); 105 (0→1); 119 (?→0).

Lusotitan atalaiensis codification for Wilson (2002) data matrix

????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ??1?? ????? ????? ????? ????? ????1 ????? ??0?? ??000 001?0 ?100? 00?00 ????? ??090&1 1?01? ????? ???01 01??1 11?10 0???? ????? ????? ???01 0?0?? ????? ??111 111?1 1110? ????? ????? ????? ???0

Lusotitan atalaiensis codification for Upchurch et al. (2004) data matrix

????? ????1 ????? ????? ????? ????? ????? ????? 0?110 1???? ????? ????? ????? ????? ????? ????1 ????? ?0&1000 ?0000 00011 01001 ??110&1 1000? ????? ????? ????? ?0&1000 ??100 1???? ????? ????? ????? ????0 ?1000 ???0? ????? ????? ???11 11111 ?1111 11??? ????? ????? ????? ????

Lusotitan atalaiensis codification for D'Emic (2012) data matrix

????? ????? ????? ?1??? ????? ????? ????? ???1? ????? ???0? ?0?00 1011? 00??0&1 01??? ????? ??00 ?0??1 ?0??? ????? ????? 1?001 1???? 00??0 0??0

Constrained analyses

- Initial constrain for outgroup topology in Upchurch *et al*. (2004): force = (1 (2 ((3 4) (5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 47 48)))).

References

D'Emic MD. 2012. The early evolution of titanosauriform sauropod dinosaurs. Zoological Journal of the Linnean Society, 166(3): 624-671.

Royo-Torres R, Upchurch P, Mannion PD, Mas R, Cobos A, Gascó F, Alcalá L, Sanz JL. 2014a. The anatomy, phylogenetic relationships and stratigraphic position of the Tithonian-Berriasian Spanish sauropod dinosaur *Aragosaurus ischiaticus*. Zoological Journal of Linnean Society, 71(3): 623-655.

Upchurch P, Barrett PM, Dodson P. 2004. Sauropoda, p. 259-322. In: Weishampel DB, Dodson P, Osmólska H. (eds.), The Dinosauria II. University Of California Press, Berkeley.
Wilson JA. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. Zoological Journal of the Linnean Society, 136: 217-276.

SUPPLEMENTARY MATERIAL 17

Measurements of SHN 181

Caudal vertebrae measurements	CdA	CdB	CdC	CdD	CdE	CdF	CdG	CdH
anteroposterior width	10,2	10,8	10,1	10,5	9,8	10,8	8,6	12, 5
mediolateral width on the anterior articulation	19,6	?	19	18,5	16,6	14,6	17,9	?
dorsovental width on the anterior articulation		?	18,5	18,4	17,6	17,3	?	?
mediolateral width on the posterior articulation	16,5*	15,7	?	?	15,7	13,9	17,5	16,9
dorsoventral width on the posterior articulation	19,6	17,5	?	?	15,4	15,8	15,4	12,5
transverse width of the left caudal rib (from the lateral face of the centrum)	?	?	10,2	?	8,2	6,5	?	?
transverse width of the right caudal rib (from the lateral face of the centrum)	?	?	8,7	?	?		?	?

Table S.43. Measurements of SHN 181 (caudal vertebrae)

Measurement	tibia
total length	74,8
proximal mediolateral width	9,3
proximal anteroposterior width	28,3*
distal mediolateral width	17*
maximum width of pvp	15
maximum width of aspa	?
shaft minimum mediolateral width	5,1
shaft minimum anteroposterior width	12,4

**measure affected by deformation*

Table S.44. Measurements of SHN 181 (tibia)

Measurement	Fibula
total length	78,6
proximal mediolateral width	4,5
proximal anteroposterior width	14,9
distal mediolateral width	7,7
distal anteroposterior width	14,4
shaft minimum mediolateral width	5,1
shaft minimum anteroposterior width	8,1
tibial suture dorsoventral width	25,1

Table S.45. Measurements of SHN 181 (fibula)

Measurement	Femur
total length	?
transverse with of the proximal end	?
transverse with of the distal end	32,5
transverse width of the diaphysis	19,2
anteroposterior width of diaphysis	7,6
anteroposterior width of the femoral head	10,3

Table S.46. Measurements of SHN 181 (femur)

Measurement	chevron
total length	23,6
transverse width of the proximal end	9,4
total length of the haemal channel	7,3
anteroposterior width of the distal end	4,7
transverse width of the distal end	12,6
haemal channel length/total length	0,31

Table S.47. Measurements of SHN 181 (chevron)

Measurement	astragalus
maximum transverse width	21,7
posterior transverse width	11,4
anteroposterior width of ascending process of astragalus	7,5
height on ascending process of astragalus	10,5

Table S.48. Measurements of SHN 181 (astragalus)

Measurement	left pubis	right pubis
length from the most anterior point in the iliac peduncle to distal end	78,6	?
anteroposterior width of proximal plate	?	?
length from the most posterior point in the iliac peduncle to distal end	79,8	?
length from the most dorsal point in the ischiatic peduncle to distal end	?	?
iliac peduncle mediolateral width	6,5	8
iliac peduncle anteroposterior width	16	?
ischiatic peduncle mediolateral width	?	?
ischiatic peduncle dorsoventral width	?	?
obturator foreman maximum diameter	?	?
obturator foreman minimum diameter	?	?
acetabulum length	?	?
anteroposterior width of the distal end	30,5	?
mediolateral width of the distal end	7,5	6,8

Table S.49. Measurements of SHN 181 (pubis)

Measurement	left ischium	right ischium
length from the most cranial point in the iliac peduncle to distal end	?	60,5
length from the most posterior point in the iliac peduncle to distal end	?	66,6
length from the most dorsal point in the pubic peduncle to distal end	?	?
length from the most ventral point in the pubic peduncle to distal end	?	?
iliac peduncle mediolateral width	?	4,9
iliac peduncle anteroposterior width	?	10,3
pubic peduncle mediolateral width	?	?
pubic peduncle dorsoventral width	?	?
transverse of the distal end	7,8	?
perpendicular width to the distal end transverse width	4,1	3,5
distal symphysis maximum length	8,4	?
acetabulum length	?	?
anteroposterior width of proximal plate	?	?
length of most posterior point in iliac peduncle to most ventral point of pubic peduncle	?	?
length of most posterior point in iliac peduncle to most ventral point of pubic peduncle	?	?
length of most anterior point in iliac peduncle to most dorsal point in pubic peduncle	?	?

All measurements in cm.

Table S.50. Measurements of SHN 181 (ischia)

SUPPLEMENTARY MATERIAL 18

Map of synapomorphies of Chapter 12 phylogenetic approach

Synapomorphies for the nodes of phylogenetic hypothesis obtained from Carballido and Sander (2014) data matrix

Node 1. No synapomorphies.

Node 2. 81 (0→1).

Node 3, Sauropoda. 141 (0→1), 168 (0→1), 232 (0→1), 261 (0→1), 328 (0→1).

Node 4. 167 (0→1), 252 (0→1), 263 (0→1).

Node 5. 299 (0→1), 300 (0→1), 336 (0→1).

Node 6. 106 (0→2).

Node 7. 232 (1→0).

Node 8. 116 (1→0).

Node 9. 300 (1→0), 341 (0→1).

Node 10, Eusauropoda. 52 (0→1), 94 (0→1), 146 (0→1), 287 (0→1), 305 (0→1), 310 (0→1), 314 (0→1), 324 (0→1), 330 (0→1), 333 (0→1), 334 (0→1), 339 (0→1), 340 (0→1).

Node 11. 118 (1→0), 182 (0→1), 230 (0→1).

Node 12. 127 (0→1), 155 (0→1), 181 (1→2).

Node 13. 161 (1→0), 164 (1→0), 310 (1→0).

Node 14. 112 (0→1), 135 (0→1), 145 (0→1), 325 (0→1).

Node 15, Mamenchisauridae. 106 (0→1), 115 (0/1/2→3), 120 (0→1/2); 124 (0→1), 125 (1→0), 126 (0→1), 139 (0→2), 152 (0→1), 174 (0→2).

Node 16. 136 (0→1), 270 (0→1), 296 (0→1), 316 (0→1).

Node 17, Turiasauria. 174 (0→1), 193 (0→2).

Node 18. 149 (0→1), 207 (0→1), 309 (0→1), 317 (0→1), 319 (0→1).

Node 19, Neosauropoda. 96 (0→1), 106 (0→2), 120 (0→1).

Node 20, Diplodocoidea. 1 (1→0), 2 (1→0), 7 (0→1), 9 (0→1), 19 (0→1), 20 (0→1), 22 (0→1), 55 (0→1), 58 (1→2), 78 (0→1), 94 (1→2), 95 (1→3), 97 (0→1), 100 (1→0), 102 (0→1), 103 (1→3), 108 (0/1→3), 145 (1→2), 163 (1→0), 184 (0→1), 199 (0→1), 205 (0→1), 215 (0→1), 219 (0→1), 220 (0→1).

Node 21, Rebbachisauridae. 203 (1→0), 208 (0→1).

Node 22. 166 (0→1), 192 (0→1).

Node 23. 152 (0→1), 193 (0→4), 289 (0→1).

Node 24. 256 (1→0), 290 (0→1), 298 (0→1).

Node 25, Limaysaurinae. 152 (1→2), 173 (0→1), 238 (0→1).

Node 26. 239 (0→1).

Node 27, Nigersaurinae. 158 (0→1), 197 (0→1), 291 (0→1), 303 (0→1).

Node 28, Flagellicaudata. 8 (0→1), 12 (1→2), 53 (1→0), 82 (0→1), 132 (0→1), 158 (0→1), 193 (0→2), 198 (0→1), 216 (1→2), 286 (0→1), 295 (1→0), 296 (1→0), 297 (0→1), 327 (0→1).

Node 29, Dicraeosauridae. 4 (0→1), 26 (0→1), 34 (1→0), 43 (0→1), 50 (0→1), 84 (0→1), 85 (0→1), 103 (3→2).

Node 30. 35 (0→1), 47 (0→1), 113 (1→0), 115 (2→1), 135 (1→0), 139 (1→0).

Node 31. 171 (0→1).

Node 32, Diplodocidae. 25 (0→1), 27 (0→1), 28 (0→1), 44 (0→1), 101 (1→0), 115 (2→3), 120 (1→2), 134 (2→3), 136 (1→0), 154 (0→1), 201 (0→1), 202 (0→1), 206 (0→1).

Node 33, Diplodocinae. 126 (0→1), 129 (0→1), 194 (0→1), 195 (0→1), 196 (0→1), 204 (0→1), 208 (0→2), 209 (0→1), 213 (2→3).

Node 34, Macronaria. 161 (1→0), 186 (0→1), 236 (0→1).

Node 35, Camarasauromorpha. 116 (1→2), 120 (1→2), 126 (0→1), 136 (1→0), 143 (0→1), 162 (0→1), 180 (0→1), 193 (0→1), 211 (0→1), 238 (0→1), 284 (0→1), 288 (0→1), 293 (0→1), 302 (0→1), 317 (1→0).

Node 36. 128 (1→0), 139 (1→2), 144 (0→1), 231 (0→1), 258 (1→0), 266 (0→1).

Node 37. 143 (1→2).

Node 38. 116 (2→3), 150 (0→1).

Node 39. 102 (0→2), 103 (1→2), 238 (1→0).

Node 40, Titanosauria. 203 (1→0).

Node 41. 148 (1→2), 155 (1→0), 216 (1→0), 217 (0→1), 294 (0→1).

Node 42, Lithostria. 118 (0→1), 149 (1→2), 151 (0→1), 152 (0→2), 157 (1→2), 311 (0→1);

Node 43. 103 (2→3), 141 (1→0), 162 (1→2), 173 (0→1), 199 (0→1), 257 (0→1).

Node 44, Nemegtosauridae. 108 (1→2).

Node 45. 30 (0→1), 61 (0→1), 70 (1→0), 77 (0→1).

Node 46. 148 (2→1), 157 (2→0).

Node 47. 150 (1→2).

Node 48. 126 (1→0).

Node 49, Saltasauridae. 140 (1→0), 195 (0→1), 244 (1→0), 246 (0→1), 256 (1→2), 264 (0→1);

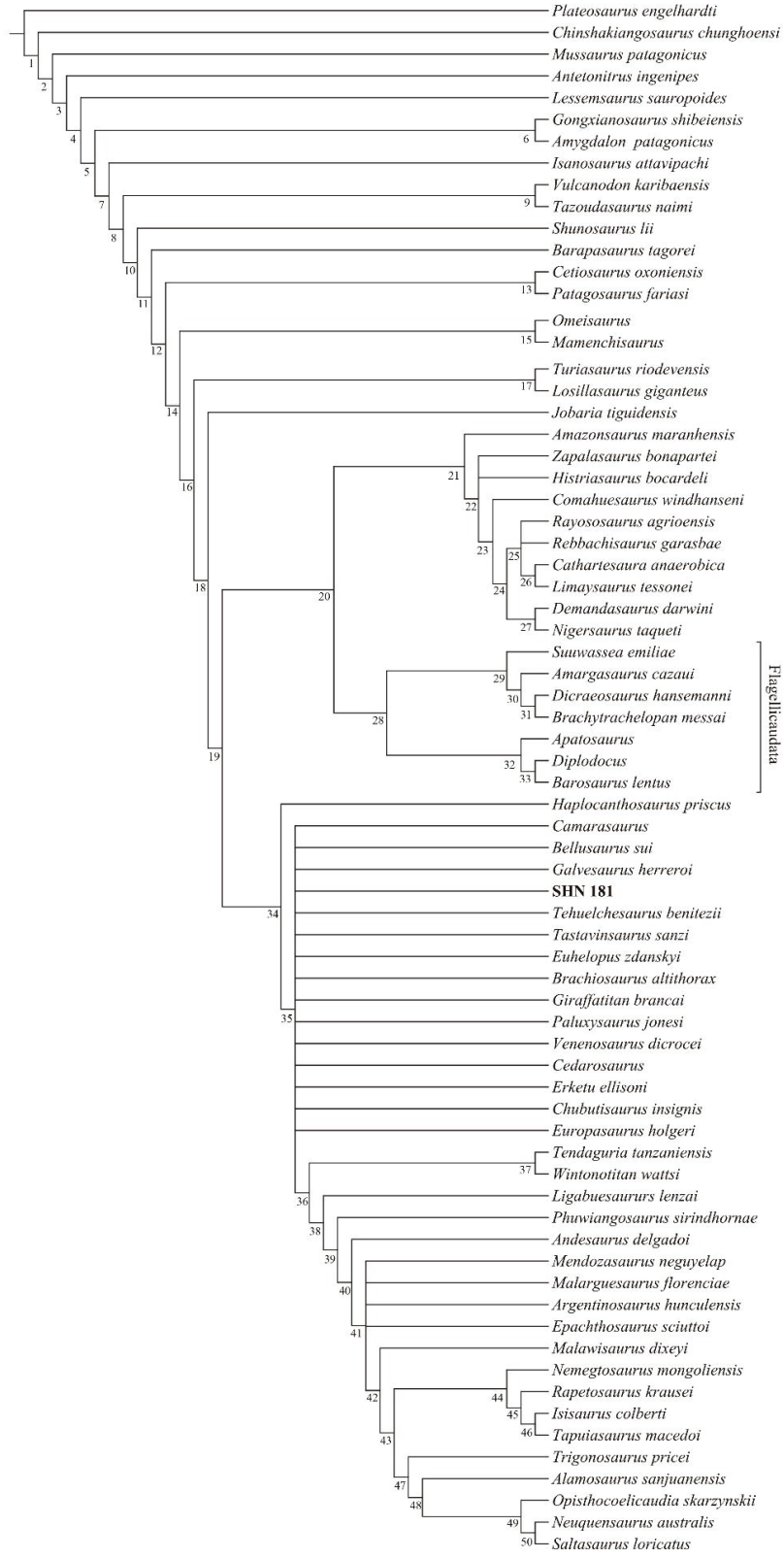
Node 50. 136 (0→1), 150 (2→1), 218 (0→1), 241 (1→0).

Note: This map of synapomorphies was obtained from the topology of consensus strictus.

References

Carballido JL, Sander PM. 2014. Postcranial axial skeleton of *Europasaurus holgeri* (Dinosauria, Sauropoda) from Upper Jurassic of Germany: implications for sauropod ontogeny and phylogenetic relationships of basal Macronaria. Journal of Systematic Paleontology, 12(3): 335-387.

Figure S.8. Phylogenetic hypothesis based on Carballido and Sander (2014) data matrix with internal nodes numbered for list of synapomorphies.


Plateosaurus engelhardti
Chinshakiangosaurus chunghoensi
Mussaurus patagonicus
Antetonitrus ingenipes
Lessemsaurus sauropoides
Gongxianosaurus shibeiensis
Amygdalon patagonicus
Isanosaurus attavipachi
Vulcanodon karibaensis
Tazoudasaurus naimi
Shunosaurus lii
Barapasaurus tagorei
Cetiosaurus oxoniensis
Patagosaurus fariasi
Omeisaurus
Mamenchisaurus
Turiasaurus riodevensis
Losillasaurus giganteus
Jobaria tiguidensis
Amazonsaurus maranhensis
Zapalasaurus bonapartei
Histriasaurus bocardeli
Comahuesaurus windhanseni
Rayososaurus agrioensis
Rebbachisaurus garasbae
Cathartesaura anaerobica
Limaysaurus tessonei
Demandasaurus darwini
Nigersaurus taqueti
Suuwassea emiliae
Amargasaurus cazaui
Dicraeosaurus hansemanni
Brachytrachelopan messai
Apatosaurus
Diplodocus
Barosaurus lentus
Flagellicaudata
Haplocanthosaurus priscus
Camarasaurus
Bellusaurus sui
Galvesaurus herreroi
SHN 181
Tehuelchesaurus benitezii
Tastavinsaurus sanzi
Euhelopus zdanskyi
Brachiosaurus altithorax
Giraffatitan brancai
Paluxysaurus jonesi
Venenosaurus dicrocei
Cedarosaurus
Erketu ellisoni
Chubutisaurus insignis
Europasaurus holgeri
Tendaguria tanzaniensis
Wintonotitan wattsi
Ligabuesaururs lenzai
Phuwiangosaurus sirindhornae
Andesaurus delgadoi
Mendozasaurus neguyelap
Malarguesaurus florenciae
Argentinosaurus hunculensis
Epachthosaurus sciuttoi
Malawisaurus dixeyi
Nemegtosaurus mongoliensis
Rapetosaurus krausei
Isisaurus colberti
Tapuiasaurus macedoi
Trigonosaurus pricei
Alamosaurus sanjuanensis
Opisthocoelicaudia skarzynskii
Neuquensaurus australis
Saltasaurus loricatus

SUPPLEMENTARY MATERIAL 19

Data matrix information for Chapter 12 phylogenetic approach

SHN 181 codification for Carballido and Sander (2014) data matrix

????? ????? ?????

SUPPLEMENTARY MATERIAL 20

List of characters

Data matrix

Skull

1. Posterolateral processes of premaxilla and lateral processes of maxilla, shape: without midline contact (0); with midline contact forming marked narial depression, subnarial foramen not visible laterally (1). (Wilson, 2002, #1).

2. Premaxillary anterior margin shape: without step (0); with marked step but short step (1); with marked and long step (2). (Carballido et al., 2012, #2).

3. Premaxilla, ascending process shape in lateral view: convex (0); concave, with a large dorsal projection (1); sub-rectilinear and directed posterodorsally (2). (Whitlock, 2011, #3).

4. Premaxilla, external surface: without anteroventrally orientated vascular grooves originating from an opening in the maxillary contact (0); vascular grooves present (1). (Whitlock, 2011, #2).

5. Maxillary border of external naris, length: short, making up much less than one-fourth narial perimeter (0); long, making up more than one third narial perimeter (1). (Wilson, 2002, #3).

6. Maxilla, foramen anterior to the preantorbital fenestra: absent (0); present (1). (Zaher et al., 2011, #244).

7. Preantorbital fenestra: absent (0); present, being wide and laterally opened (1). (Carballido et al., 2012, #2).

8. Subnarial foramen and exterior maxillary foramen, position: well distanced from one another (0); separated by narrow bony isthmus (1). (Wilson, 2002, #5)

9. Antorbital fenestra: much shorter than orbital maximum diameter, less than 85% of orbit (0); subequal to orbital maximum diameter, greater than 85% orbit (1). (Whitlock, 2011, #13).

10. Antorbital fenestra, shape of dorsal margin: straight or convex (0); concave (1). (Whitlock, 2011, #14).

11. Antorbital fossa: present (0); absent (1). (Wilson, 2002, #7).

12. External nares position: terminal (0); retracted to level of orbit (1); retracted to a position between orbits (2). (Wilson, 2002, #8).

13. External nares, maximum diameter: shorter (0); or longer than orbital maximum diameter (1). (Wilson, 2002, #9).

14. Orbital ventral margin, anteroposterior length: broad, with subcircular orbital margin (0); reduced, with acute orbital margin (1). (Wilson, 2002, #10).

15. Lacrimal, anterior process: present (0); absent (1). (Wilson, 2002, #11).

16. Jugal contribution to the ventral border of the skull: present (0); absent (1). (Carballido et al., 2012, #16).

17. Quadratojugal-Maxila contact: absent or small (0); broad (1). (Whitlock, 2011, #10).

18. Jugal-ectopterygoid contact: present (0); absent (1). (Wilson, 2002; #12).

19. Jugal, contribution to antorbital fenestra: very reduced or absent (0); large, bordering approximately one-third its perimeter (1). (Wilson, 2002, #13).

20. Quadratojugal, position of anterior terminus: posterior to middle of orbit (0); anterior margin of orbit or beyond (1). (Whitlock, 2011, #30).

21. Quadratojugal, anterior process length: short, anterior process shorter than dorsal process (0); long, anterior process more than twice as long as dorsal process (1). (Wilson, 2002, #32).

22. Quadratojugal, angle between anterior and dorsal processes: less than or equal to 90°, so that the quadrate shaft is directed dorsally (0); greater than 90°, approaching 130°, so that the quadrate shaft slants posterodorsally (1). (Whitlock, 2011, #31).

23. Ventral edge of anterior surface of the quadratojugal: straight, not expanded ventrally (0); concave due to a ventral expansion of the anterior region (1). (Upchurch et al., 2004, #26).

24. Squamosal contribution to the supratemporal fenestra: present, the squamosal is well visible in dorsal view (0); reduced or absent (1). (Curry Rogers, 2005, #37).

25. Squamosal-quadratojugal contact: present (0); absent (1). (Wilson, 2002, #31).

26. Squamosal, posteroventral margin: smooth (0); with prominent, ventrally directed "prong" (1). (Whitlock, 2011, #37).

27. Prefrontal posterior process size: small, not projecting far posterior of frontal-nasal suture (0); elongate, approaching parietal (1). (Wilson, 2002, #14).

28. Prefrontal, posterior process shape: flat (0); hooked (1). (Wilson, 2002, #15).

29. Prefrontal, anterior process: absent (0); present (1). (Curry Rogers, 2005, #30).

30. Prefrontal-Frontal contact width: large, equal or longer that the anteroposterior length of the prefrontal (0); narrow, less than half the anteroposterior length of the prefrontal (1). (Zaher et al., 2011, #239).

31. Postorbital, ventral process shape: transversely narrow (0); broader transversely than anteroposteriorly (1). (Wilson, 2002, #16).

32. Postorbital, posterior process: present (0); absent (1). (Wilson, 2002, #17).

33. Postorbital, posterior margin articulating with the squamosal: with tapering posterior process (0); with a deep posterior process (1). (Zaher et al., 2011; #245).

34. Frontal contribution to supratemporal fossa: present (0); absent (1). (Wilson, 2002, #18).

35. Frontals, midline contact (symphysis): sutured (0); or fused in adult individuals (1). (Wilson, 2002, #19).

36. Frontal, anteroposterior length: approximately twice (0); or less than minimum transverse breadth (1). (Wilson, 2002, #20).

37. Frontal-nasal suture, shape: flat or slightly bowed anteriorly (0); V-shaped, pointing posteriorly (1). (Whitlock, 2011, #21).

Comment: The region between the nasals in *Kaatedocus* (Tschopp and Mateus, 2013) and *Spinophorosaurus nigerensis* (Knoll et al., 2012) is posteriorly retracted resembling the V-shaped suture present in *Limaysaurus* and *Nigersaurus* (Sereno et al., 2007). Nevertheless, in both skull, the nasal are not preserved (*Kaatedocus*, Tschopp and Mateus, 2013; *S. nigerenis*, pers. observ. PM, contra Remes et al., 2009). Tschopp et al. (2015) considered as different condition, and raised a new feature (#29) in order to include the condition present by *Kaatedocus*, SMA0011 and *S. nigerensis* being scored herein as "?", following those authors.

38. Frontals, dorsal surface: without paired grooves facing anterodorsally (0); grooves present, extend on to nasal (1). (Whitlock, 2011, #22).

39. Frontal, contribution to dorsal margin of orbit: less than 1.5 times the contribution of prefrontal (0); at least 1.5 times the contribution of prefrontal (1). (Whitlock, 2011, #23).

40. Frontal, medial convexity in dorsal view: absent (0); present (1) (Curry Rogers, 2005, #33).

41. Parietal occipital process, dorsoventral height: short, less than the diameter of the foramen magnum (0); deep, nearly twice the diameter of the foramen magnum (1). (Wilson, 2002; #21).

42. Parietal, contribution to post-temporal fenestra: present (0); absent (1). (Wilson, 2002, #22).

43. Parietal, distance separating supratemporal fenestrae: less than (0); or twice the long axis of supratemporal fenestra (1). (Wilson, 2002, #24).

44. Parietal, elongate posterolateral process: present (0); absent (1) (Mannion et al., 2013, #84).

45. Postparietal foramen: absent (0); present (1). (Wilson, 2002, #23).

46. Paroccipital process distal terminus: straight, slightly expanded surface (0); rounded, tongue-like process (1). (Whitlock, 2011, #42).

47. Supratemporal fenestra: present (0); absent (1). (Wilson, 2002, #25).

48. Supratemporal fenestra, long axis orientation: anteroposterior (0); transverse (1). (Wilson, 2002, #26).

49. Supratemporal fenestra, maximum diameter: much longer than (0); or subequal to that of foramen magnum (1). (Wilson, 2002, #27).

50. Supratemporal region, anteroposterior length: temporal bar longer (0); or shorter anteroposteriorly than transversely (1). (Wilson, 2002, #28).

51. Supratemporal fossa, lateral exposure: not visible laterally, obscured by temporal bar (0); visible laterally, temporal bar shifted ventrally (1). (Wilson, 2002, #29).

52. Supraoccipital, sagittal nuchal crest: broad, weakly developed (0); narrow, sharp and distinct (1). (Whitlock, 2011, #45).

53. Laterotemporal fenestra, anterior extension: posterior to orbit (0); ventral to orbit (1). (Wilson, 2002, #30).

54. Quadrate fossa: absent (0); present (1). (Wilson, 2002, #33).

55. Quadrate fossa, depth: shallow (0); deeply invaginated (1). (Wilson, 2002, #34).

56. Quadrate fossa, orientation: posterior (0); posterolateral (1). (Wilson, 2002, #35).

57. Quadrate, articular surface shape: quadrangular in ventral view, oriented transversely (0); roughly triangular in shape or thin, crescent-shaped surface with anteriorly directed medial process (1). (Mannion et al., 2012, #29).

58. Quadrate, articular surface shape: quadrangular in ventral view, oriented transversely or roughly triangular in shape (0); thin, crescent-shaped surface with anteriorly directed medial process (1). (Mannion et al., 2012, #30).

59. Quadrate, dorsal margin: concave, such that pterygoid flange is distinct from quadrate shaft (0); straight, without clear distinction of posterior extension of pterygoid flange (1). (Tschopp et al., 2015, #53).

60. Quadrate, posterior end (posterior to posterior-most extension of pterygoid ramus): short and robust (0); elongate and slender (1) (Tschopp et al., 2015, #54).

61. Palatobasal contact, shape: pterygoid with small facet (0); dorsomedially orientated hook (1); or rocker-like surface for basipterygoid articulation (2). (Wilson, 2002, #36).

62. Pterygoid, transverse flange (i.e. ectopterygoid process) position: posterior of orbit (0); between orbit and antorbital fenestra (1); anterior to antorbital fenestra (2). (Wilson, 2002, #37).

63. Pterygoid, quadrate flange size: large, palatobasal and quadrate articulations well separated (0); small, palatobasal and quadrate articulations approach (1). (Wilson, 2002, #38).

64. Pterygoid, palatine ramus shape: straight, at level of dorsal margin of quadrate ramus (0); stepped, raised above level of quadrate ramus (1). (Wilson, 2002, #39).

65. Pterygoid, sutural contact with ectopterygoid: broad, along the medial or lateral surface (0); narrow, restricted to the anterior tip of the ectopterygoid (1). (Zaher et al. 2011, #240).

66. Palatine, lateral ramus shape: plate-shaped (long maxillary contact) (0); rod-shaped (narrow maxillary contact) (1). (Wilson, 2002, #40).

67. Epipterygoid: present (0); absent (1). (Wilson, 2002, #41).

68. Vomer, anterior articulation: maxilla (0); premaxilla (1). (Wilson, 2002, #42).

69. Supraoccipital, height: twice sub-equal to (0); or less than height of foramen magnum (1). (Wilson, 2002, #43; Carballido et al., 2012, #65).

70. Paroccipital process, ventral non-articular process: absent (0); present (1). (Wilson, 2002, #44).

71. Crista prootica, size: rudimentary (0); expanded laterally into dorsolateral process (1). (Wilson, 2002, #45).

72. Basipterygoid processes, length: short, approximately twice (0); or elongate, at least four times basal diameter (1). (Wilson, 2002, #46).

73. Basipterygoid processes, angle of divergence: approximately 45° (0); less than 30° (1). (Wilson, 2002, #47).

74. Basal tubera, anteroposterior depth: approximately half dorsoventral height (0); sheet-like, 20% dorsoventral height (1). (Wilson, 2002, #48).

75. Basal tubera, breadth: much broader than (0); or narrower than occipital condyle (1). (Wilson, 2002, #49).

76. Basal tubera: distinct from basipterygoid (0); reduced to slight swelling on ventral surface of basipterygoid (1). (Whitlock, 2011, #53).

77. Basal tubera, shape of posterior face: convex (0); slightly concave (1). (Whitlock, 2011, #54).

78. Basioccipital depression between foramen magnum and basal tubera: absent (0); present (1). (Wilson, 2002, #50).

79. Basisphenoid/basipterygoid recess: present (0); absent (1). (Wilson, 2002, #51).

80. Basisphenoid/quadrate contact: absent (0); present (1). (Wilson, 2002, #52).

81. Basisphenoid, sagital ridge between basipterygoid processes: absent (0); present (1). (Zaher et al., 2011, #242).

82. Basipterygoid processes, orientation: perpendicular to (0); or angled approximately 45° (1) to the skull roof. (Wilson, 2002, #53).

83. Basipterygoid, area between the basipterygoid processes and parasphenoid rostrum: is a mildly concave subtriangular region (0); forms a deep slot-like cavity that passes posteriorly between the bases of the basipterygoid processes (1). (Mannion et al., 2012, #48).

84. Occipital region of skull, shape: anteroposteriorly deep, paroccipital processes oriented posterolaterally (0); flat, paroccipital processes oriented transversely (1). (Wilson, 2002, #54).

85. Dentary, depth of anterior end of ramus: slightly less than that of dentary at midlength (0); 150% minimum depth (1). (Wilson, 2002, #55).

86. Dentary, anteroventral margin shape: gently rounded (0); sharply projecting triangular process (1). (Wilson, 2002, #56).

87. Dentary symphysis, orientation: angled 15° or more anteriorly to (0); or perpendicular to axis of jaw ramus (1). (Wilson, 2002, #57).

88. Dentary, cross-sectional shape of symphysis: oblong or rectangular (0); subtriangular, tapering sharply towards ventral extreme (1); subcircular (2). (Whitlock, 2011, #60).

89. Dentary, tuberosity on labial surface near symphysis: absent (0); present (1). (Whitlock, 2011, #57).

90. Dentary posteroventral process, shape: single (0); forked (1) (Chure et al., 2010, #43).

91. Mandible, coronoid eminence: strongly expressed, clearly rising above plane of dentigerous portion (0); absent (1). (Whitlock, 2011, #62).

92. External mandibular fenestra: present (0); absent (1). (Wilson, 2002, #58).

93. Surangular depth: less than twice (0); or more than two and one-half times maximum depth of the angular (1). (Wilson, 2002, #59).

94. Surangular ridge separating adductor and articular fossae: absent (0); present (1). (Wilson, 2002, #60).

95. Adductor fossa, medial wall depth: shallow (0); deep, prearticular expanded dorsoventrally (1). (Wilson, 2002, #61).

96. Splenial posterior process, position: overlapping angular (0); separating anterior portions of prearticular and angular (1). (Wilson, 2002, #62).

97. Splenial posterodorsal process: present, approaching margin of adductor chamber (0); absent (1). (Wilson, 2002, #63).

98. Coronoid, size: extending to dorsal margin of jaw (0); reduced, not extending dorsal to splenial (1); absent (2). (Wilson, 2002, #64).

99. Tooth rows, shape of anterior portions: narrowly arched, anterior portion of tooth rows V-shaped (0); broadly arched, anterior portion of tooth rows U-shaped (1); rectangular, tooth-bearing portion of jaw perpendicular to jaw rami (2). (Wilson, 2002, #65).

100. Tooth rows, length: extending to orbit (0); restricted anterior to orbit (1); restricted anterior to antorbital fenestra (2); restricted anterior to subnarial foramen (3). (Carballido et al., 2012, #95).

101. Dentary teeth, number: greater than 20 (0); 10-17 (1); 9 or fewer (2). (Carballido et al., 2012, #96).

102. Replacement teeth per alveolus, number: two or fewer (0); more than four (1). (Wilson, 2002, #74).

103. Lateral plate: absent (0); present (1). (Upchurch et al., 2004, #9).

104. Teeth, orientation: perpendicular (0); or oriented anteriorly relative to jaw margin (1). (Wilson, 2002, #75).

105. Tooth crowns, orientation: aligned along jaw axis, crowns do not overlap (0); aligned slightly anterolingually, tooth crowns overlap (1). (Wilson, 2002, #69).

106. Crown-to-crown occlusion: absent (0); present (1). (Wilson, 2002, #67).

107. Occlusal pattern: interlocking, V-shaped facets (0); high-angled planar facets (1); low-angled planar facets (2). (Wilson, 2002, #68).

108. Tooth crowns, cross-sectional shape at mid-crown: elliptical (0); D-shaped (1); cylindrical (2). (Wilson, 2002, #70).

109. Enamel surface texture: smooth (0); wrinkled (1). (Wilson, 2002, #71).

110. Thickness of enamel asymmetric labiolingually: absent (0); present (1). (Whitlock, 2011, #74).

111. Marginal tooth denticles: present (0); absent on posterior edge (1); absent on both anterior and posterior edges (2). (Carballido et al., 2012, #106).

112. Teeth, longitudinal grooves on lingual aspect: absent (0); present (1). (Wilson, 2002, #76).

113. SI values for tooth crowns: less than 3.0 (0); 3.0-4.0 (1); 4.0-5.0 (2); more than 5.0 (3). (Carballido et al., 2012, #108).

114. Maxillary teeth, shape: straight along axis (0); twisted axially through an arc of 30-45° (1). (D'Emic, 2012, #15).

Cervical vertebrae

115. Cervical vertebrae, number: 10 or fewer (0); 12 (1); 13-14 (2); 15 (3); 16 or more (4). (Carballido et al., 2012, #109).

116. Atlantal neural arch: without foramen (0); with foramen (1). (Whitlock, 2011, #85).

117. Atlas, intercentrum occipital facet shape: rectangular in lateral view, length of dorsal aspect subequal to that of ventral aspect (0); expanded anteroventrally in lateral view, anteroposterior length of dorsal aspect shorter than that of ventral aspect (1). (Wilson, 2002, #79).

118. Cervical centra, articulations: amphicoelous (0); opisthocoelous (1). (Salgado et al., 1997, #1).

119. Cervical centra, ventral surface: is flat or slightly convex transversely (0); transversely concave (1). (Upchurch, 1998, #84).

120. Cervical centra, midline keels on ventral surface: prominent and plate-like (0); reduced to low ridges or absent (1). (Upchurch, 1998, #83).

This is a difficult character to codified, being complicated to evaluate what is a marked or rudimentary ventral crest. Several taxa bears a ventral crest in their respective ventral faces, such as *Spinophorosaurus*, *Dicraeosaurus*, *Nigersaurus* (MNHN material) or *Dinheirosaurus*. The usage of the anterior dorsal vertebrae is complicated, because here, the crest become more pronounced,

fact that could be related with the transition between cervical and dorsal series. Nevertheless, this part of the neck is particular rare in sauropods, being difficult to compare the behavior of this feature in the transition between caudal and dorsal series. The presence of the primitive character is recognized in *Dicraeosaurus*, *Nigersaurus*, *Amargasaurus*, and other taxa. In *Nigersaurus* and *Dicraeosaurus* this crest seems to be more pronounced and long anteroposteriorly.

121. Cervical vertebrae, height divided width (measured in its posterior articular surface): higher than 1.1 (0), around 1 (1); between 0.9 and 0.7 (2); smaller than 0.7 (3). (Carballido et al., 2012, #116).

122. Cervical vertebrae, neural arch lamination: well developed, with well-marked laminae and fossae (0); rudimentary, with diapophyseal laminae absent or very slightly marked (1). (Wilson, 2002, #81).

123. Postaxial cervical centra, parapophyses dorsally excavated: absent (0); present (1) (Mannion et al., 2013, #121).

124. Cervical centra, internal pneumaticity: absent (0); present with singles and wide cavities (1); present, with several small and complex internal cavities (2) (Carballido et al., 2012, #120).

125. Postaxial cervical centra, lateral surfaces: lack an excavation or have a pleurocoel no posteriorly defined (0); well-defined pleurocoel, including the posterior margin laminae (1) (modified from Carballido et al., 2012, #114).

126. Cervical vertebrae, small fossa on posteroventral corner: absent (0); shallow, anteroposteriorly elongate fossa present, posteroventral to pleurocoel (1) (Tschopp et al., 2015, #131).

127. Middle and posterior cervical vertebrae, parapophyses, shape: subcircular or only slightly longer than tall (0); elongate, making up more than half the functional centrum length in posterior cervical vertebrae (1) (D'Emic, 2012, #28).

128. Middle cervical vertebrae, parapophyses, shape and orientation: weakly developed, project laterally or slightly ventrally from the centrum (0); broad and project ventrally such that cervical ribs are displaced ventrally more than the height of the centrum (1). (D'Emic, 2012, #29).

129. Anterior cervical parapophyses: arises at mid-centrum (0); arises in anterior half of centrum (1) (Curry Rogers, 2005, #121).

130. Posterior-most cervical vertebrae, region between centrum and prezygapophyses, height: tall, around centrum height (0); low, much less than centrum height (1). (D'Emic, 2012, #34).

131. Cervical neural arches, epipophyses present on postzygapophyses: absent (0); present (1) (Mannion et al., 2013, #127).

132. Cervical vertebrae, epipophyses, shape: stout, pillar-like expansions above postzygapophyses (0); posteriorly projecting prongs (1). (D'Emic, 2012, #24).

Comment: This feature should be observe in middle cervical vertebrae (or, not so recommended, on posterior cervical vertebrae).

133. Cervical vertebrae, "epipophyseal-prezygapophyseal" lamina (eprl), morphology: absent (0); subvertical (variable in slope) (1), subhorizontal (a true eprl) (2) (modified from D'Emic, 2012, #25 and Carballido et al., 2012, #119).

Comment. In *Lourinhasaurus* was reported the presence of an "eprl" lamina on a fragment of the posterior cervical neural spines (Mocho et al., 2014). According its fragmentary state, this features is scorer as "?" for this taxon.

134. Cervical vertebrae, intrapostzygapophyseal lamina, shape: has little or no relief past margin of centropostzygapophyseal lamina (cpol) when viewed laterally (0); projects beyond cpol in lateral view, with distinct 'kink' (1) (D'Emic, 2012, #26).

135. Anterior cervical vertebrae, prespinal lamina: absent (0); present (1). (Carballido et al., 2012, #121).

136. Anterior cervical vertebrae, neural spine shape: single (0); bifid (1). (Wilson, 2002, #72).

137. Middle cervical neural spines, shape: single (0); bifid (1) (D'Emic, 2012, #22).

138. Mid-cervical neural spines, orientation: vertical (0); anteriorly inclined (1). (Tschopp et al., 2015, #169).

139. Posterior cervical vertebrae, neural spine shape: without a great lateral expansion (0); laterally expanded, being equal or wider than the vertebral centrum (1) (Carballido et al., 2012, #131).

140. Middle and posterior cervical vertebrae, prespinal lamina: absent (0); present (1). (Carballido et al., 2012, #123).

141. Middle cervical vertebrae, lateral fossae on the prezygapophysis process: absent (0); present (1). (Carballido et al., 2012, #124).

142. Middle cervical vertebrae, height of the neural arch: less than the height of the posterior articular surface (0); higher than the height of the posterior articular surface (1). (Wilson, 2002, 87).

143. Middle cervical centrum, anteroposterior length divided the height of the posterior articular surface: less than 4 (0); more than 4 (1). (Wilson, 2002, #74).

Comment: In the absence of complete series, in particular, on the middle sector, the absence of an EI less than 4 do not guarantee accurately the absence of the apomorphic state. In these cases, we recommend the scoring of this feature as "0", although should be taken with some caution. This is the situation of *Dinheirosaurus lourinhanensis* holotype (Bonaparte and Mateus, 1999; Mannion et al., 2012), which only preserve the two most posterior cervical vertebrae (should be scored as "?") or *Huabeisaurus allocotus*, with a very complete cervical series (D'Emic et al., 2013).

144. Middle and posterior cervical vertebrae, morphology of the centroprezygapophyseal lamina (cprl): single (0); dorsally divided, resulting in a lateral and medial lamina, being the medial lamina linked with the intraprezygapophyseal lamina and not with the prezygapophysis (1); divided, resulting in the presence of a "true" divided centroprezygapophyseal lamina, which is dorsally connected to the prezygapophysis (2). (Carballido et al., 2012, #127).

145. Middle and posterior cervical vertebrae, morphology of the centropostzygapophyseal lamina (CPOL): single (0); divided, with the medial part contacting the intrapostzygapophyseal lamina (1). (Carballido et al., 2012, #128).

146. Middle and posterior cervical vertebrae, articular surface of zygapophyses: flat (0); transversally convex (1). (Carballido et al., 2012, #129).

147. Posterior cervical vertebrae, lateral profile of the neural spine: displays steeply sloping anterior and posterior faces (0); displays steeply sloping anterior face and noticeably less steep posterior margin (1). (Upchurch et al., 2004, #119).

148. Posterior cervical and anterior dorsal vertebrae, neural spine, shape: single (0); bifid (1); (modified from D'Emic, 2012, #32).

149. Posterior cervical and anterior dorsal bifid neural spines, median tubercle: absent (0); present (1) (Carballido et al., 2012, #133).

150. Middle cervical vertebrae, angle between postzygodiapophyseal and spinopostzygapophyseal laminae: acute (0); approximately 90º (1). (Sereno et al., 2007, #56)

151. Middle cervical diapophyses, prominent triangular flange on posterior edge of diapophyseal process: absent (0); present (1) (modified from Remes et al., 2009, #78).

152. Mid- and posterior cervical vertebrae, lateral edge posterior to parapophysis: continuous (0); marked by a deep groove extending anteroposteriorly along the edge (1). (Tschopp et al., 2015).

153. Posterior cervical and anterior dorsal vertebrate, roughened lateral aspect of prezygodiapophyseal lamina: absent (0); present (1) (Whitlock, 2011, #102).

154. Posterior cervical neural spines, dorsoventrally elongate coel on lateral surface posteriorly to the spinoprezygapophyse lamina (sprl): absent (0); present (1). (modified from Mannion et al., 2012, #99).

155. Posterior cervical vertebrae, subvertical lamina extending between the ventral surface of the postzygodiapophyseal lamina and the dorsal surface of the posterior centrodiapophyseal lamina: absent (0); present (1) (Mannion et al., 2012, #95).

156. Posterior cervical neural arches, accessory spinal lamina: absent (0); present, running vertically just posterior to spinoprezygapophyseal lamina (sprl) (1). (Mannion et al., 2012, #98).

Comment. This is not the same lamina described in the feature #133. Feature #133, discriminate into three states the absence and the presence of a subhorizontal lamina (eprl) or a subvertical lamina (probably not homologues). This lamina is considered a different lamina that generally appears behind the sprl (parallel to sprl) and posteriorly bordering the fossa described by character #154. *Kaatedocus*, for example, present this fossa, but the posterior edge is free from any type of laminae (Tschopp and Mateus, 2013).

157. Posterior cervical and anterior dorsal bifid neural spines, orientation: diverging (0); parallel to converging (1). (Tschopp et al., 2015, #211).

158. Middle cervical vertebrae, relative height between the neural spine and epipophyses (or postzygapophyses when the epipophyses is absent): neural spine higher (0); similar heights, (1). (NEW).

159. Middle cervical neural spines, abrupt increase in height (height approximately doubled), following low anterior cervical neural spines (occurs around Cv6–8): absent (0); present (1). (Mannion et al., 2013, #134).

160. Mid-posterior cervical prezygapophyses, pre-epipophyses process situated ventrolaterally to articular surface, absent (0); present (1). (modified from Remes et al., 2009, #79).

161. Transition between middle and posterior cervical vertebrae, anterior projection of the dorsal end of the sprl, well visible in lateral view: absent (0); present (1) (based on Tschopp and Mateus, 2013).

Cervical ribs

162. Cervical ribs, distal shafts of longest cervical ribs: are elongate and form overlapping bundles (0); are short and do not project beyond the posterior end of the centrum to which they are attached (1). (Wilson, 2002, #140).

163. Cervical ribs, angle between the capitulum and tuberculum: greater than 90°, so that the rib shaft lies close to the ventral edge of the centrum (0); less than 90°, so that the rib shaft lies below the ventral margin of the centrum (1). (Wilson, 2002, #139).

Dorsal vertebrae

164. Number of dorsal vertebrae: 14 or more (0); 13 (1); 12 (2); 10 (3). (Carballido et al., 2012, #134).

165. Dorsal centra, pleurocoels: absent (0); present (1). (Wilson, 2002, #78).

166. Dorsoventral compressed pleurocoels acquiring an 'eye-shaped' morphology: absent (0); present (1). (Salgado et al., 1997, #20).

167. Dorsal centra, lateral pneumatic foramina are: shallow fossae or excavations that do not ramify throughout the centrum (0); deep excavations that ramify throughout the centrum and into the base of the neural arch, often leaving only a thin septum on the midline of the centrum (1) (Mannion et al., 2013, #144).

168. Dorsal vertebrae, transverse processes: are directed laterally or slightly upwards (0); are directed strongly dorsolaterally (1). (Upchurch et al., 2004, #138).

169. Dorsal vertebrae, distal end of the transverse process: curves smoothly into the dorsal surface of the process (0); is set off from the dorsal surface, the latter having a distinct dorsally facing flattened area (1). (Upchurch et al., 2004, #140).

170. Dorsal vertebrae, non-bifid neural spine in anterior or posterior view: possess subparallel lateral margins (0); possess lateral margins which slightly diverge dorsally (1); possess lateral margins which strongly diverge dorsally (2). (Carballido et al., 2012, #138).

171. Dorsal centra, pneumatic structures: absent, dorsal centra with solid internal structure (0); present, dorsal centra with simple and big air spaces (1); present, dorsal centra with small and complex air spaces (2). (Carballido et al., 2012, #139).

172. Anterior and middle dorsal neural spines, spinoprezygapophyseal lamina (sprl): absent (0); present (1). (Carballido et al., 2012, #140).

173. Posterior dorsal neural spines, spinoprezygapophyseal lamina (SPRL): absent (0); present (1). (Carballido et al., 2012, #141).

174. Dorsal vertebrae, single not bifid neural spines, single prespinal lamina (PRSL): absent (0); present (1). (Carballido et al., 2012, #142).

175. Dorsal vertebrae, single not bifid neural spines, single prespinal lamina (prsl): rough and wide, present in the dorsalmost part of the neural spine (0); rough and wide, extended through almost all the neural spine (1); smooth and narrow (2). (Carballido et al., 2012, #143)

176. Dorsal vertebrae with single neural spines, middle single fossa projected thought the midline of the neural spine: present (0); absent (1). (Carballido et al., 2012, #144).

177. Dorsal vertebrae with single neural spines, middle single fossa (sprf), projected through the midline of the neural spine: relatively wide medial simple fossa (0); a thin median simple fossa (occupying all dorsal extension of the neural spine or near ½) (1); extremely reduced median simple fossa (only located at the base) (2). (modified from Carballido et al., 2012, #145).

178. Anterior dorsal centra, articular face shape: amphicoelous (0); opisthocoelous (1). (Wilson, 2002, #94).

179. Middle dorsal neural arches in lateral view, anterior edge of the neural spine: project anteriorly to the diapophysis (0); converge with the diapophysis (1); project posteriorly to the diapophysis (2). (Carballido et al., 2012, #148).

180. Anterior and middle dorsal vertebrae, zygapophyseal articulation angle: horizontal or slightly posteroventrally oriented (0); posteroventraly oriented (around 30º) (1); strongly posteroventraly oriented (more than 40º) (2). (Carballido et al., 2012, #149).

181. Middle to posterior dorsal centra, ventral surface: convex transversely (0); flattened (1); is slightly concave, sometimes with one or two crests (2). (Carballido et al., 2012, #150).

182. Middle dorsal vertebrae, hyposphene-hypantrum system: present (0); absent (1). (Carballido et al., 2012, #151).

183. Posterior dorsal vertebrae, hyposphene-hypantrum system: present and well developed, usually with a rhomboid shape (0); present and weakly developed, mainly as a laminar articulation (1); absent or only present in posteriormost dorsal vertebrae (2). (Carballido et al., 2012, #152).

184. Mid- and posterior dorsal vertebrae, accessory lamina linking hyposphene with base of posterior centrodiapophyseal lamina (pcdl): absent (0); present (1). (modified from Tschopp et al., 2015, #260).

Comment. It should be scored as "0" when the hyposphene is absent.

185. Middle and posterior dorsal vertebrae with a single lamina (the single tpol) supporting the hyposphene or postzygapophysis from below: absent (0); present (1). (Carballido et al., 2012, #154).

186. Middle and posterior dorsal vertebrae, transverse processes length: short (0); long (projecting along 1.5 the articular surface width) (1). (Carballido et al., 2012, #153).

187. Middle and posterior dorsal vertebrae, neural channel in anterior view: entirely surrounded by the neural arch (0); enclosed in a deep fossa, enclosed laterally by pedicels (1). (Upchurch et al., 2004, #136).

188. Middle and posterior dorsal vertebrae, neural spine height: approximately twice the centrum length (0); for times the centrum length (1). (Carballido et al., 2012, #156).

189. Middle and posterior dorsal neural spines orientation: vertical (0); slightly inclined, with an angle of around 70 degrees (1); strongly inclined, with an angle not bigger than 40 degrees (2). (Carballido et al., 2012, #157).

190. Middle and posterior dorsal neural arches, centropostzygapophyseal lamina (cpol), shape simple (0); divided (1). (Wilson, 2002, #95).

191. Middle and posterior dorsal neural arches, anterior centroparapophyseal lamina (acpl): absent (0); present (1). (Wilson, 2002, #96).

192. Middle and posterior dorsal neural arches, prezygoparapophyseal lamina (prpl): absent (0); present (1). (Wilson, 2002, #97).

193. Middle and posterior dorsal neural arches, posterior centroparapophyseal lamina (pcpl): absent (0); present (1). (Wilson, 2002, #98).

194. Mid- and posterior dorsal neural arches, posterior centroparapophyseal lamina (pcpl): absent (0); present as single lamina (1); present, double (2) (modified from Tschopp et al., 2015, #258).

195. Middle and posterior dorsal centrum in transverse section (height: width ratio): subcircular (ratio, similar to 1 or a bit higher) (0); slightly dorsoventrally compressed (ratios between 0.8 and 1) (1); strongly compressed (ratios below 0.8) (2). (Carballido et al., 2012, #162).

196. Middle and posterior dorsal vertebrae neural spine, triangular aliform processes: absent (0); present but do not project far laterally (not as far as postzygapophyses) (1); present and project far laterally (as far as postzygapophyses) (2). (Carballido et al., 2012, #163).

197. Middle and posterior dorsal vertebrae, spinodiapophyseal lamina (spdl): absent (0); present (1). (Upchurch et al., 2004, #157).

198. Middle and posterior dorsal vertebrae, accessory spinodiapophyseal lamina: absent (0); present (1). (Upchurch et al., 2004, #151).

199. Dorsal vertebrae, spinodiapophyseal webbing: lamina follows curvature of neural spine in anterior view (0); lamina "festooned" from spine, dorsal margin does not closely follow shape of neural spine and diapophysis (1). (Whitlock, 2011, #104).

200. Anterior dorsal vertebrae, spinopostzygapophyseal lamina (spol): absent (0); present (1). (Upchurch et al., 2007, #133).

201. Middle and posterior dorsal neural spines, lateral spinopostzygapophyseal lamina (lat. spol): absent (0); present (1). (Wilson, 2002, #100).

202. Middle and posterior dorsal neural arches, spinodiapophyseal lamina (spdl) and spinopostzygapophyseal lamina (lat. spol) contact: absent (0); present (1). (Wilson, 2002, #101).

203. Middle and posterior dorsal vertebrae, spinodiapophyseal (spdl) and spinopostzygapophyseal lamina (lat. spol) contact: ventral, well separated from the triangular aliform process (0); dorsal, forms part of the triangular aliform process (1). (Carballido et al., 2012, #170).

204. Middle and posterior dorsal vertebrae, height of neural arch below the postzygapophyses (pedicel): less than height of centrum (0); subequal to or greater than height of centrum (1). (Whitlock, 2011, #109).

205. Posterior dorsal vertebrae, medial spinopostzygapophyseal lamina (med. spol): absent (0); present and forms part of the median posterior lamina (1). (modified from Carballido et al., 2012, #172).

Comment. Sometimes the lat. spol might develops an internal fossa (spol.f). In this character, we only considered as med. spol, a lamina medially located, individualized from the lat. spol, only connected we this lamina above the postzygapophyses.

206. Posterior dorsal neural arches, postspinal lamina (posl) or posl+med. spol: wide, shallow and rough (0); medially restricted and occupying and occupying the dorsoventral height of neural spine (1); medially restricted and occupying and occupying the dorsoventral height of neural spine, ventrally bifurcated (2) (modified from Mannion et al., 2012, #122).

207. Dorsal (single) neural spines, postspinal lamina (posl), dorsal end: flat to convex transversely (0); concave transversely (1). (Tschopp et al., 2015, #234).

208. Posterior dorsal vertebrae, transverse processes: lie posterior, or posterodorsal, to the parapophysis (0); lie vertically above the parapophysis (1). (Upchurch et al., 2004, #139).

209. Posterior dorsal centra, articular face shape: amphicoelous (0); slightly opisthocoelous (1); opisthocoelous (2). (Carballido et al., 2012, #174).

210. Posterior dorsal vertebrae, neural spine: narrower transversely than anteroposteriorly (0); broader transversely than anteroposteriorly (1). (Wilson, 2002, #92).

211. Posterior dorsal vertebra, posterior centrodiapophyseal lamina (pcdl): has an unexpanded ventral tip (0); expands and may bifurcate toward its ventral tip (1). (Carballido et al., 2012, #176).

212. Middle dorsal vertebrae, postzygadiapophyseal lamina (podl): present (0); absent (1). (D'Emic, 2012, #42).

213. Dorsal neural arches, posterior face, paired and subdivided pneumatic chambers dorsolateral to neural canal: absent (0), present (1) (modified from Whitlock, 2011, #106).

214. Middle dorsal neural spines, form: single, bifid form (if present) does not extend past the second or third dorsal (0); bifid, inclusive of at least the fifth dorsal vertebrae (1). (Whitlock, 2011, #108).

215. Dorsal margin of anterior or middle dorsal non-bifid neural spines with a concave dorsal margin (bifurcations are considered as concave): absent (0); present (1). (NEW).

216. Middle and posterior dorsal neural arches: height above postzygapophyses (neural spine) equal to height below (pedicel) (0); neural spine much taller than pedicel (1) (Whitlock 2011, #114).

217. Dorsal neural spine (not including arch), height: less than two times centrum length (0); two times centrum length (1); four times centrum length (2) (Whitlock, 2010, #118).

218. Anterior dorsal neural spines, orientation: project dorsally or slightly anterodorsally (0); project posterodorsally (1) (Mannion et al., 2013, #160).

219. Dorsal neural spines, anteroposterior width: approximately constant along the height of the spine, with subparallel anterior and posterior margins (0); narrows dorsally to form a triangular shape in lateral view, with the base approximately twice the width of the dorsal tip (1). (Mannion et al., 2013, #159).

220. Dorsal neural spines, height: anterior dorsal neural spines subequal to or dorsoventrally shorter than posterior dorsal neural spines (0); anterior dorsal neural spines dorsoventrally taller than posterior dorsal neural spines (1) (Mannion et al., 2013, #158).

221. Posterior dorsal neural spines, orientation at its base: vertical (0); anteriorly inclined (1). (Tschopp et al., 2015, #280).

Dorsal ribs

222. Dorsal ribs, proximal pneumatopores: absent (0); present (1). (Wilson, 2002, #141).

223. Anterior dorsal ribs, cross-sectional shape: sub-circular (0); plank-like, anteroposterior breadth more than three times mediolateral breadth (1). (Wilson, 2002, #142).

Sacral vertebrae

224. Sacral vertebrae, number:: 3 or fewer (0); 4 (1); 5 (2); 6 or more (3). (Wilson, 2002, #108).

225. Sacrum, sacricostal yoke: absent (0); present (1). (Wilson, 2002, #109).

226. Sacral vertebrae contributing to acetabulum: numbers 1-3 (0); numbers 2-4 (1). (Wilson, 2002, #110).

227. Sacral neural spines length: approximately twice length of centrum (0); approximately four times length of centrum (1). (Wilson, 2002, #111).

228. Sacral ribs, dorsoventral length: low, not projecting beyond dorsal margin of ilium (0); high extending beyond dorsal margin of ilium (1). (Wilson, 2002, #112).

229. Sacral vertebrae, pleurocoels in the lateral surfaces of sacral centra: absent (0); present (1). (Upchurch et al., 2004, 165).

230. Sacral vertebrae, camellate internal tissue structure: absent (0); present (1). (Mannion et al., 2013, #172).

Caudal vertebrae

231. Caudal vertebrae, number: 35 or fewer (0); 40 to 55 (1); increased to 70-80 (2). (Wilson, 2002, #114).

232. Caudal bone texture: solid (0); spongy, with large internal cells (1). (Wilson, 2002, #113).

233. Caudal ribs: persist through caudal 20 or more posteriorly (0); disappear by caudal 15 (1); disappear by caudal 10 (2). (Wilson, 2002, #115).

234. First caudal centrum or last sacral vertebra, articular face shape: flat (0); procoelous (1); opisthocoelous (2); biconvex (3). (Wilson, 2002, #116).

235. First caudal neural arch, coel on lateral aspect of neural spine: absent (0); present (1). (Wilson, 2002, #117).

236. Anterior caudal vertebrae, caudal rib: ventral surface directed laterally or slightly ventrally (0); directed dorsally (1). (Whitlock, 2011, #125).

237. Proximalmost anterior caudal vertebrae, caudal ribs, ventral lamina with a kink visible in anteroposterior views: absent (0); present (1). (modified from Chure et al., 2010; #87).

238. Proximal caudal vertebrae, round and deep fossa just below the postzygapophyses: absent (0); present (1) (based on González Riga, 2003).

239. Proximal anterior caudal vertebrae with a continuous prezygodiapophyseal lamina and well-developed cprf: absent (0); present (1) (modified from Ksepka and Norell, 2010, #240).

240. Anterior caudal centra (excluding the first), articular face shape: amphiplatyan or amphicoelous (0); procoelous/distoplatyan (1); slightly procoelous (2); procoelous (3); posterior surface markedly more concave than the anterior one (4). (Carballido et al., 2012, #193).

241. Apex of the convexity of the posterior articulation on anterior and middle caudal vertebrae: concentrically or slightly displaced above the centrum midline (0); strongly displaced upward, so that the apex of the posterior articulation is flushed to the level of the dorsal margin of the centrum (1). (Santucci and Arruda-Campos, 2011, #235).

242. Anterior margin of the anterior caudal vertebrae: vertical (0); strongly inclined forward (1) (Santucci and Arruda-Campos, 2011, #236).

243. Anterior caudal centra, pleurocoels: absent (0); present (1). (Wilson, 2002, #119).

Comment. This character is restricted fossae with well developed margins, i.e. true pleurocoels, as occur in SHN (JJS) 177 or Diplodocus (Hatcher, 1901).

244. Anterior caudal vertebrae, blind fossae in lateral centrum: absent (0); present, often sporadically along the vertebral series (1) (modified from D'Emic, 2012, #56).

Comment. These blind fossae are shallow depression more or less individualized without the emargination of the border, i.e. they are not true pleurocoels. The taxa with pleurocoels are scored as "-" (inapplicable).

245. Proximal anterior caudal vertebrae, ventral surfaces: convex transversely (0); concave transversely (1). (modified from Upchurch et al., 2004, #182).

246. Anterior and middle caudal vertebrae, well-developed ventrolateral ridges: absent (0); present (1). (modified from Upchurch et al., 2004, #183).

247. Anterior and middle caudal centra, ventral longitudinal hollow: absent (0); present (1). (Wilson, 2002, #132).

248. Anterior caudal prezygapophyses, pre-epipophysis laterally below articular facet: absent (0); present (1). (Tschopp et al., 2015, #311).

249. Anterior and middle caudal vertebrae, triangular lateral process on the neural spine: absent (0); present (1). (Whitlock, 2011, #123).

250. Anterior or middle caudal vertebrae, sagittal crest on the ventral concavity when is present: no ventral concavity or absent (0); present (1) (based on Powell, 1992, 2003).

251. Anterior caudal vertebrae, caudal ribs shape: triangular, tapering distally (0); "wing-like", not tapering distally (1). (Wilson, 2002, #128).

252. Anterior caudal vertebrae (not including the most proximal caudal vertebrae), caudal ribs, orientation: roughly perpendicular (0); swept backwards, usually reaching posterior margin of centrum (excluding posterior ball if present) (1) (D'Emic, 2012, #59).

253. Anterior caudal neural spines, transverse breadth: approximately 50% of (0); or greater than anteroposterior length (1). (Wilson, 2002, #126).

254. Anterior caudal neural spines, anteroposteriorly well developed prespinal (prsl) and postspinal (posl) laminae with an appreciable section visible in lateral view: absent (0); present and mainly laminar, prespinal is much more developed laminae (1); present and rough (2). (NEW).

255. Prezygapophyses curved downward on anteriormost caudal vertebrae: absent (0); present (1). (Santucci and Arruda-Campos, 2011, #238).

256. Anterior caudal vertebrae, caudal ribs, proximal depth: shallow, on centrum only (0); deep, extending from centrum to neural arch (1). (Wilson, 2002, #127).

257. Anterior caudal vertebrae, caudal ribs, diapophyseal laminae (acdl, pcdl, prdl, podl): absent (0); present (1). (Wilson, 2002, #129).

258. Anterior caudal vertebrae, caudal ribs, anterior centrodiapophyseal lamina (acdl), shape: single (0); divided (1). (Wilson, 2002, #130).

259. Anterior caudal vertebrae, hyposphene ridge: absent (0); present (1). (Upchurch et al., 2004, #187).

260. Anterior caudal centra, length: approximately the same (0); or doubling over the first 20 vertebrae (1). (Wilson, 2002, #120).

261. Anterior caudal neural arches, spinoprezygapophyseal lamina (sprl): absent, or present as small short ridges that rapidly fade out into the anterolateral margin of the spine (0); present, extending onto lateral aspect of neural spine (1). (Carballido et al., 2012, #205).

262. Anterior caudal neural arches, spinoprezygapophyseal lamina (sprl)-spinopostzygapophyseal lamina (spol) contact: absent (0); present, forming a prominent lamina on lateral aspect of neural spine (1). (Wilson, 2002, #122).

263. Anterior caudal neural arches, prespinal lamina (prsl): absent (0); present (1). (Wilson, 2002, #123).

264. Anterior caudal neural spines, postspinal lamina (posl) coming from the dorsal area of the neural spine: absent or wide (0); medial restricted (1). (NEW).

265. Caudal neural spines, elliptical depression between spinodiapophyseal lamina (spdl) and postspinal lamina on lateral neural spine: absent (0); present (1). (Mannion et al., 2012, #127).

266. Anterior caudal neural spines, shape: single (0); dorsally bifurcated (1) (modified from Whitlock 2011, #139).

267. Anterior caudal neural spines, shape: single or slightly concave in anterior view (0); well-developed bifurcation dorsally bifurcated (1) (NEW).

268. Anterior caudal neural spines (not including arch), height: less than 1.5 times centrum height (0); 1.5 times centrum height or more (1) (Whitlock, 2011, #126).

269. Anterior caudal vertebrae, concavo-convex zygapophyseal articulation: absent (0); present (1) (Whitlock, 2011, #143).

270. Articular facets of the prezygapophyses on anterior and middle caudal vertebrae: normal, not expanded (0); wide, with a dorsal and a ventral expansion or protuberance (1). (Santucci and Arruda-Campos, 2011, #237).

271. Middle caudal centra, shape: cylindrical (0); quadrangular, flat ventrally and laterally (1). (modified from Wilson, 2002, #131).

272. Middle caudal centra, articular face shape: amphiplatyan or amphicoelous (0); procoelous/distoplatyan (1); slightly procoelous (2); procoelous (3). (Carballido et al., 2012, #210).

273. Middle caudal vertebrae, location of the neural arches: over the midpoint of the centrum with approximately sub-equal amounts of the centrum exposed at either end (0); on the anterior half of the centrum (1). (Upchurch et al., 2004, #185).

274. Middle caudal vertebrae, orientation of the neural spines: anteriorly (0); vertical (1); slightly directed posteriorly (2); strongly directed posteriorly (3). (Carballido et al., 2012, #213).

275. Postzygapophyses located on the anterior half of the centrum on anterior and middle caudal vertebrae: absent (0); present (1). (Santucci and Arruda, 2011, #239).

276. Length proportions of the prezygapophyses with respect to the centrum length in middle caudal vertebrae: less than 40% (0); between 40-50% (1); more than 50% (2). (Santucci and Arruda-Campos, 2011, #241).

277. Middle caudal vertebrae, ratio of centrum length to centrum height: less than 2, usually 1.5 or less (0); 2 or higher (1). (Upchurch et al., 2004, #179).

278. Anterior-most posterior caudal vertebrae (those with still well-developed neural spine), neural spine orientation: vertical (0); slightly directed posteriorly (1); strongly directed posteriorly (2). (Carballido et al., 2012, #216).

279. Posterior caudal centra, articular face shape: amphyplatic (0); procoelous (1); opisthocoelous (2). (Carballido et al., 2012, #217).

Comment: The status of the *Mendozasaurus* posterior caudal vertebrae (González Riga, 2003) of are here considered as amphyplatic, although the presence of a small circular convexity on the dorsal section of the posterior articulation, reminiscent of the procoelous articulation present in the middle and anterior caudal vertebrae. The same condition is also found in *Paludititan* (Csiki et al., 2010) and *Malawisaurus* (Gomani, 2005), and so, scored as "0".

280. Posterior caudal centra, shape: cylindrical (0); dorsoventrally flattened, breadth at least twice height (1). (Wilson, 2002, #135).

281. Posterior caudal vertebrae, ratio of length to height: less than 5, usually 3 or less (0); 5 or higher (1). (Upchurch et al., 2004, #180).

282. Distalmost caudal centra, articular face shape: platycoelous (0); biconvex (1) (Wilson, 2002, #136).

283. Distalmost biconvex caudal centra, number: 10 or fewer (0); more than 30 (1). (Wilson, 2002, #137).

284. Distalmost caudal centra, length-to height ratio: less than 4 (0); greater than 5 (1). (Carballido et al., 2012, #222).

285. Pleurocoels in middle or posterior vertebrae: absent (0); present (1). (NEW)

286. Proximal caudal vertebrae, centrum height: circular or dorsoventrally high (0); dorsoventrally compressed (1). (NEW)

287. Anterior caudal vertebrae, centrum height (excluding the most proximal ones): circular or dorsoventrally high (0); dorsoventrally compressed (1). (NEW)

288. Middle-to-posterior caudal vertebrae, centrum height: circular or dorsoventrally high (0); dorsoventraly compressed (1). (NEW)

289. Middle caudal vertebrae, the presence of a bony process separating the postzygapophyses from the neural spine: absent (0); present (1). (based on Calvo and González Riga, 2003).

Haemal arches

290. Forked chevrons with anterior and posterior projections: absent (0); present (1). (Wilson, 2002, #143).

291. Forked chevrons, distribution: distal tail only (0); throughout middle and posterior caudal vertebrae (1). (Wilson, 2002, #144).

292. Chevrons, crus bridging dorsal margin of haemal canal: present (0); absent (1). (Wilson, 2002, #145).

293. Chevron haemal canal, depth: short, approximately 25% (0); or long, approximately 50% chevron length (1). (Wilson, 2002, #146).

294. Chevrons: persisting throughout at least 80% of tail (0); disappearing by caudal 30 (1). (Wilson, 2002, #147.).

295. Posterior chevrons, distal contact: fused (0); unfused (open) (1). (Wilson, 2002, #14).

296. Anterior and middle chevrons, articular facets: contiguous (0); composed by to facets (1) (modified from D'Emic, 2012, #66).

297. Haemal arches with double articular facets set in a concave posterodorsal surface: absent (0); present (1). (Santucci and Arruda-Campos, 2011, #240).

298. First chevron, morphology: Y-shaped and does not differ notably from subsequent chevrons (0); anteroposteriorly flattened and V-shaped, with dorsoventrally reduced distal blade (1). (Mannion et al., 2013, #207).

Scapular girdle

299. Scapular acromion process, size: narrow (0); broad, width more than 150% minimum width of blade (1). (Wilson, 2002, #150).

300. Scapula, acromion process dorsal margin: concave or straight (0); with V/U-shaped concavity (1) (modified from Carballido et al., 2012, #233).

301. Scapular blade, orientation respect to coracoid articulation: perpendicular (0); forming a 45º angle (1). (Wilson, 2002, #151).

302. Scapular blade, shape: acromial edge not expanded (0); rounded expansion on acromial side (1); racquet-shaped (2). (Wilson, 2002, #152).

303. Scapula, highest point of the dorsal margin of the blade: lower than the dorsal margin of the proximal end (0); at the same height than the dorsal margin of the proximal end (1); higher than the dorsal margin of the proximal end (2). (Carballido et al., 2012, #234).

304. Scapula, development of the acromion process: undeveloped (0); well-developed (1). (Carballido et al., 2012, #235).

305. Scapular length/minimum blade breadth: 5.5 or less (0); 5.5 or more (1). (Carballido et al., 2012, #236).

306. Scapular, acromial process position: lies nearly glenoid level (0); lies nearly midpoint scapular body (1). (Carballido et al., 2012, #238).

307. Scapular acromion length: less than 1/2 scapular length (0); at least 1/2 scapular length (1). (Mannion et al. 2012, #168).

308. Glenoid scapular orientation: relatively flat or laterally facing (0); strongly beveled medially (1). (Wilson, 2002, #153).

309. Scapular blade, cross-sectional shape at base: flat or rectangular (0); D-shaped (1). (Wilson, 2002, #154).

310. Portion of the proximal scapular expansion lying behind the acromial ridge: flat or convex and decreases in transverse thickness toward its free edge (0), forms a separate excavated area (1). (Upchurch et al., 2004, #202).

311. Dorsal margin of the coracoid in lateral view: reaches or surpasses the level of the dorsal margin of the scapular expansion (0); lies below the level of the scapular proximal expansion and separated from the latter by a V-shaped notch (1). (Upchurch et al., 2004, #207).

312. Coracoid, infraglenoid deep groove: absent (0); present (1). (Carballido et al., 2012, #245).

313. Coracoid, infraglenoid lip: absent (0); present (1). (Wilson, 2002, #157).

314. Coracoid, anteroventral margin shape: rounded (0); rectangular (1). (Wilson, 2002, #156).

315. Coracoid, proximodistal length: less than the length of scapular articulation (0); approximately twice the length of scapular articulation (1). (Wilson, 2002, #155).

316. Coracoid, shape: anteroposterior dimension more than 1.5 times proximodistal dimension (0); anteroposterior dimension less than proximodistal dimension (1). (D'Emic, 2012, #73).

317. Cranial and dorsal margins of the coracoid in lateral view: merge smoothly into each other, giving a rounded profile (0); meet each other at an abrupt angle, making the coracoid subquadrangular in outline (1). (Upchurch et al., 2004, #208).

318. Sternal plate, shape: oval (0); crescentic (1). (Wilson, 2002, #158).

319. Prominent posterolateral expansion of the sternal plate producing a kidney-shaped profile in dorsal view: absent (0); present (1). (Upchurch et al., 2004, #211).

320. Prominent parasagittal oriented ridge on the dorsal surface of the sternal plate: absent (0); present (1). (Upchurch et al., 2004, #212).

321. Ridge on the ventral surface of the sternal plate: absent (0); present (1). (Upchurch et al., 2004, #213).

322. Sternal plate length/humerus length: about 0.5 (0); more than 0.7 (1) (D'Emic, 2012, #77).

Forelimb

323. Humerus-to-femur ratio: less than 0.60 (0); 0.60 to 0.90 (1); >0.90 (2). (Upchurch et al., 2004, #216).

324. Humeral deltopectoral attachment, development: prominent (0); reduced to a low crest or ridge (1). (Wilson, 2002, #160).

325. Humeral deltopectoral attachment projection: anteriorly or slightly medially (0); medially (1). (NEW).

326. Reduced deltopectoral attachment shape: raise from the dorsal margin, becoming progressively more pronounced (0); constricted dorsalventrally, becoming laterally pointed (1) (NEW, based on Royo-Torres et al., 2006).

327. Humeral deltopectoral crest, shape: relatively narrow throughout length (0); markedly expanded distally (1). (Wilson, 2002, #161).

328. Humeral midshaft cross-section, shape: circular (0); elliptical (1). (Mannion et al., 2012, #170).

329. Humeral distal condyles, articular surface shape: restricted to distal portion of humerus (0); exposed on anterior portion of humeral shaft (1). (Wilson, 2002, #163).

330. Humeral distal condyle, shape: divided (0); flat (1). (Wilson, 2002, #164).

331. Humeral proximolateral corner, shape: rounded, the dorsal surface is well convex (0); pronounced / square, the dorsal surface low, almost flat (1). (Wilson, 2002, #159).

332. Humeral, lateral margin: medially deflected (0); almost straight until the half-length or even more (1). (Carballido et al., 2012, #259).

333. Humerus, strong posterolateral bulge on around level of the deltopectoral crest: absent (0); present (1). (modified from D'Emic, 2012, #80).

334. Humerus, strong posterolateral bulge on around level of the deltopectoral crest visible in anterior view: absent (0); present (1). (modified from D'Emic, 2012, #80).

335. Humerus, RI (sensu Wilson and Upchurch, 2003): Gracile (less than 0.27) (0); medium (0.28-0.32) (1); Robust (more than 0,33) (2). (Carballido et al., 2012, #256).

336. Humerus, proportions: breadth of proximal endless (0) equals or more (1) than 50% of the humeral length (González Riga et al., 2009, #75).

337. Distalmost part of the posterior surface of the humerus: shallowly concave (0), deeply concave between the lateral and medial prominent vertical ridges (1) (Upchurch et al., 2004, #221).

338. Humerus, lateroproximal corner dorsally pronounced: absent (0); present (1). (NEW).

339. Humerus, medially deflected proximal end [(width from the sagittal plan to the mediodorsal border of the proximal end/total mediolateral width of the proximal end measure at the mediodorsal border level)x100]: less than 70% (0); more than 70%, close to 80% (1). (NEW, based on Royo-Torres et al., 2006 and Barco, 2009).

340. Ulnar proximal condyle, shape: subtriangular (0); triradiate, with deep radial fossa (1). (Upchurch, 1998, #161).

341. Ulnar proximal condylar processes, relative lengths: sub-equal (0); unequal, anterior arm longer (1). (Wilson, 2002, #166).

342. Ulnar olecranon process, development: prominent, projecting above proximal articulation (0); rudimentary, level with proximal articulation (1). (Wilson, 2002, #167).

343. Ulna, length-to-proximal breadth ratio: gracile (0); stout (1) (Wilson, 2002, #168).

344. Anteromedial process of the proximal end of the ulna: has a strongly concave proximal surface (0); has a flat proximal surface (1) (Upchurch, 1998, #161).

345. Radial distal condyle, shape: round (0); subrectangular, flattened posteriorly and articulating in front of ulna (1). (Wilson, 2002, #169).

346. Radius, distal breadth: slightly larger than (0) or approximately twice (1) midshaft breadth. (Wilson, 2002, #170).

347. Radius, distal condyle orientation: perpendicular to (0) or beveled approximately 20 ° proximolaterally (1) relative to long axis of shaft. (Wilson, 2002, #171).

348. Carpal bones, number: 3 or more (0); 2 or fewer (1). (Upchurch, 1998, #163).

349. Carpal bones, shape: round (0); block-shaped, with flattened proximal and distal surfaces (1). (Wilson and Sereno, 1998, #42).

350. Metacarpus, shape: spreading (0); bound, with subparallel shafts and articular surfaces that extend half their length (1). (Wilson and Sereno, 1998, #80).

351. Metacarpals, shape of proximal surface in articulation: gently curving, forming a 90° arc (0); U-shaped, subtending a 270 ° arc (1). (Wilson and Sereno, 1998, #81).

352. Longest metacarpal-to-radius ratio: close to 0.3 (0); 0.45 or more (1). (Wilson and Sereno, 1998, #93).

353. Metacarpal I, length: shorter than (0) or longer than (1) metacarpal IV. (Wilson and Sereno, 1998, #94).

354. Metacarpal I, distal condyle shape: divided (0); undivided (1). (Wilson, 2002, #179).

355. Metacarpal I distal condyle, transverse axis orientation: beveled approximately 20° proximodistally (0) or perpendicular (1) with respect to axis of shaft. (Wilson, 2002, #180).

356. Manual digits II and III, phalangeal number: 2-3-4-3-2 or more (0); reduced, 2-2-2-2-2 or less (1); absent or un-ossified (2). (Wilson, 2002, #181).

357. Manual phalanx I.1, shape: rectangular (0); wedge-shaped (1). (Wilson, 2002, #182).

358. Manual non-ungual phalanges, shape: longer proximodistally than broad transversely (0); broader transversely than long proximodistally (1). (Wilson and Sereno, 1998, #44).

359. Metacarpal I: shorter than metacarpals II or III (0), longer than metacarpals II or III, i.e., metacarpal I is the longest metacarpal (1). (Upchurch, 1998, #166).

360. Ungual on manual digit I: large, at least 50% of metacarpal I length (0), reduced, less than 25% of metacarpal I length, or absent (absence can be assessed from the reduced and grooveless articular surface of phalanx I) (1). (Upchurch et al., 2004, #240).

361. Metacarpal V: highly reduced or absent (0), large, at least 90% of the length of the longest metacarpal (1). (Upchurch et al., 2004, #234).

362. Triangular, striated areas for ligament attachment on the proximal parts of the metacarpal shafts: absent (0), present (1). (Upchurch et al., 2004, #236).

363. Metacarpal IV, articulation for metacarpal V, shape: anteroposteriorly long, broad articular surface (0); articular surface forms a near right angle, transverse and anteroposterior dimensions of proximal end sub-equal (1) (D'Emic, 2012, # 93).

364. Metacarpals, metacarpal IV has a prominent proximolateral projection that wraps around the dorsal (anterior) face of metacarpal V (metacarpal IV often forms a chevron shape in proximal end view): absent (0); present (1) (Mannion et al., 2013, #241).

365. Metacarpals, distal articular surfaces: extend onto dorsal/anterior surface of metacarpal (0); restricted to distal surface (except sometimes in metacarpal IV) (1) (D'Emic, 2012, #96).

Pelvic girdle

366. Ilium, ischial peduncle size: large, prominent (0); low, rounded (1). (Wilson, 2002, #185).

367. Ilium, dorsal margin shape: flat (0); semicircular (1). (Wilson, 2002, #186).

368. Ilium, preacetabular process shape: pointed, arching ventrally (0); semicircular, with posteroventral excursion of cartilage cap (1). (Wilson, 2002, #188).

369. Ilium, preacetabular process orientation: anterolateral to body axis (0); perpendicular to body axis (1). (Wilson, 2002, #189).

370. Postacetabular process of the ilium: lies in an approximately vertical plane (0), turns laterally toward its ventral tip to form a horizontal portion (1). (Upchurch et al., 2004, #243)

371. Highest point on the dorsal margin of the ilium: lies posteriorly to the base of the pubic process (0); lies posteriorly to the base of the pubic process (1). (Upchurch et al., 2004, #245).

372. Pelvis, anterior breadth: narrow, ilia longer anteroposteriorly than distance separating preacetabular processes (0); broad, distance between preacetabular processes exceeds anteroposterior length of ilia (1). (Wilson, 2002, #184).

373. Ilium, pubic peduncle, shape: anteroposterior and transverse dimensions sub-equal (0); transverse dimension more than 1.5 times anteroposterior dimension (1). (D'Emic, 2012, #100).

374. Ilium, preacetabular process, kink on ventral margin: absent (0); present (1). (D'Emic, 2012, #99).

375. Projected line (chord) connecting articular surfaces of ischiatic and pubic processes of ilium: passes ventral-to-ventral margin of postacetabular portion of ilium (0); passes through or dorsal to ventral edge of postacetabular portion of ilium (1) (Upchurch et al., 2004, #249).

376. Ilium, pneumatized: absent (0); present (1). (Mannion et al., 2013, #249).

377. Maximum height of iliac blade (should be verified using the perpendicular line with the development axis of the iliac blade): posteriorly or at to the base of the pubic peduncle (0); anteriorly to the base of pubic peduncle (in the preacetabular region) (1). (NEW).

378. Lateral protuberance above the ischiatic articulation: absent (0); present (1) (NEW, based on Poropat et al., 2015).

379. Pubis length respect to ischium: pubis slightly smaller or sub-equal to the ischium (0); pubis larger (around 120% or more) than the ischium (1). (Carballido et al., 2012, #285).

380. Pubis, ambiens process development: small, confluent with (0) or prominent, projecting anteriorly from (1) anterior margin of pubis (Wilson, 2002, #189).

Comment. Instead an well developed ambiens process, some taxa bears a rough triangular crest (e.g. SHN 181). This morphology should be scored as "0".

381. Pubic apron, shape: flat (straight symphysis) (0); canted anteromedially (gentle S-shaped symphysis) (1). (Wilson, 2002, #190).

382. Puboischial contact, length: approximately one third total length of pubis (0); one-fourth total length of pubis or more (1). (Wilson, 2002, #191).

383. Middle and distal portions of the pubis: lie in a transverse plane, while the proximal end lies in a parasagittal plane (0), lie in the same plane as the proximal end, this plane being craniolaterally to caudomedially oriented (1) (Upchurch et al., 2004, #252).

384. Ischial blade, shape: emarginated distal to pubic peduncle (0); no emargination distal to pubic peduncle (1). (Wilson, 2002, #193).

385. Ischial blade emargination: deep (0); smooth and unpronounced (1). (NEW).

386. Ischia pubic articulation: less or equal to the anteroposterior length of pubic pedicel (0); greater than the anteroposterior length of pubic pedicel (1). (Carballido et al., 2012, #293).

387. Ischial distal shafts, cross-sectional shape: V-shaped, forming an angle of nearly 50º with each other (0); flat, nearly coplanar (1). (Wilson, 2002, #195).

388. Ischia, distal end: is only slightly expanded (0); is strongly expanded dorsoventrally (1). (Upchurch, 1998, #183).

389. Ischium, elongate muscle scar on proximal end: absent (0); present (1). (Whitlock, 2011, #174).

390. Ischium, tubercle on lateroventral face, shape: set in fossa (0); raised on surface (1). (D'Emic, 2012, #106).

Comment: The tuberculum might be not well-developed, but the presence of a fossa seems to be constant in the plesiomorphic state. The absence of a fossa should be scored as "1".

391. Ischium, acetabular margin, shape (in lateral view): flat or mildly concave (0); strongly concave (markedly circular), such that the pubic articular surface forms an anterodorsal projection (1) (Mannion et al., 2013, #251).

392. Symphysis between the ischia: terminates at the base of the proximal plates (0), extends along the ventral edges of the proximal plates, as well as the distal shafts, so that there is no V-shaped gap between the proximal ends of the ischiatic peduncle in dorsal view (1). (Upchurch et al., 2004, #254).

393. Ischium, acetabular articular surface: maintains approximately the same transverse width throughout its length (0); is transversely narrower in its central portion and strongly expanded as it approaches the iliac and pubic articulations (1). (Mannion et al., 2012, # 180).

394. Ischia, anteroposterior pubic pedicel width divided the total length of the ischium: less than 0,5 (0); 0,5 or more. (modified from Carballido et al., 2012, #294).

395. Extension of the ventral margin of the ischiatic peduncle divided to the total length of the pubic articulation: 2 or greater (0); lesser than 2 (1). (NEW).

396. Ischiatic distal shaft, shape: (0) triangular, depth of ischiatic shaft increases medially; (1) bladelike, medial and lateral depths sub-equal. (Upchurch et al., 2004, 194).

397. Angle between the ischiatic penduncle and the acetabulum: higher than 60º (0); acute, 60º or lesser (1). (NEW).

Hindlimb

398. Femur, fourth trochanter development: prominent (0); reduced to crest or ridge (1); extremely reduced (2). (Whitlock, 2011, #186).

399. Femur in lateral view: convex (0); straight (1). (Salgado et al., 1997; #4).

400. Fourth trochanter on femur: is situated on the posterior surface, near the midline of the shaft (0); is situated on the caudomedial margin of the shaft (1) (Upchurch, 1998, #189).

401. Media deflection of proximal 1/3 of the femur, marked by a break of slope: absent (0), present (1) (Wilson and Sereno, 1998, #100).

402. Development of lateral expansion of proximal 1/3, the distance from a straight line that contains the greater trochanter and the lateral point of the femoral shaft where it reaches its minimum transverse width up to parallel that comprises the outest point of the lateral bulge: less than 30 percent (0) or 30% or more (1) the minimum transverse width of the shaft (based on Salgado et al., 1997).

403. With the femoral shaft on vertical, the tibia condyle is ventromedial projected, relatively to the fibular condyle: absent (0); present (1). (NEW).

404. Lateral deflection of femoral shaft, position of the point between the line which pass through the ventral tip of the tibial and fibular condyle and the line which parts from greater trochanter: lateral or coincident (0) or medial to the most lateral point of the femoral distal section (1). (NEW).

405. Femur, robusticity (minimum midshaft transverse width: femur total length, with midshaft in a vertical position): gracile, midshaft width:femoral length < 0.15 (0); robust, mid-shaft width:femoral length > 0.15 (1). (Curry-Rogers, 2005, #333),

406. Lesser trochanter on the femur: is well-developed (0); is absent or greatly reduced (1). (Upchurch, 1998, #188).

407. Middle and lower portions of the femoral shaft in posterior view: have a sigmoid curve (0), straight (1). (Upchurch et al., 2004, #264).

408. Femoral mid-shaft, transverse diameter: sub-equal to (0), 125–150%, or (1) at least 185% (2) anteroposterior diameter. (Wilson, 2002, #198).

409. Femoral distal condyles, relative transverse breadth: subequal (0); tibial much broader than fibular (1). (Wilson, 2002, #200).

410. Femoral distal condyles, orientation relatively to the femoral shaft: perpendicular or slightly bevelled dorsolaterally (0) or bevelled dorsomedially approximately 10° (1). (Wilson, 2002, #201).

411. Femoral distal condyles, articular surface shape: restricted to distal portion of femur (0); expanded onto anterior portion of femoral shaft (1). (Wilson, 2002, #202).

412. Profile of the fourth trochanter in lateral/medial view: asymmetrical and pointed (0); rounded and symmetrical (1). (Upchurch et al., 2007, #242).

413. Femur, pronounced trochanter shelf: absent (0); present (1). (based on Whitlock, 2011, #181 and Otero, 2010).

414. Rough crest with position of linea intermuscularis cranialis on the anterior face of the femur shaft: absent (0) present (1). (Mannion et al., 2013, #257).

415. Tibia, proximal condyle, shape: narrow, long axis anteroposterior (0); expanded transversely, condyle subcircular (1). (Wilson, 2002, #203).

416. Tibia, distal breadth: approximately 125% (0); more than twice mid-shaft breadth (1). (Wilson, 2002, #205).

417. Proximal section in dorsal view: the cnemial crest is pronounced and projected from the articulation for the fibula (0), not pronounced and projected from the articular surface of the fibula (1). (NEW).

418. Ratio of tibial:femoral length: >0.6 (0); <0.6 (1) (modified based in Upchurch et al., 2004, #273).

419. Tibial cnemial crest, orientation: projecting anteriorly (0); or laterally (1). (Wilson, 2002, #204).

420. Fibula, proximal tibial scar, development: not well-marked (0); well-marked and deepening anteriorly (1). (Wilson, 2002, #207).

421. Fibula, lateral trochanter: absent (0); present (1). (Wilson, 2002, #208).

422. Fibula, lateral trochanter: weak developed (0); pronounced in anterior/posterior view (1). (NEW).

423. Fibular lateral muscle scar: oval in outline (0), formed from two vertically elongate parallel ridges (1). (Upchurch et al., 2004, #281).

424. Fibula, shaft in lateral view: straight (0); sigmoidal (1). (Mannion et al., 2013, #274).

425. Fibular distal condyle, size: sub-equal to shaft (0); expanded transversely, more than twice the mid-shaft breadth (1). (Wilson, 2002, #209).

426. Fibula, proximal end, anterior crest: absent or poorly developed (0); well developed, creating interlocking proximal crus (1). (D'Emic, 2012, #111).

427. Fibula in proximal view: lateral trochanter not markedly projected nor pointed (0); pointed and projected (1). (NEW).

428. Astragalus, foramina at base of ascending process: present (0); absent (1). (Wilson, 2002, #201).

429. Astragalus, shape: rectangular or with medial part slight constricted (0); wedge-shaped, with reduced anteromedial corner, medial part constricted (1). (Wilson, 2002, #210).

430. Astragalus in proximal view: widens (0) or narrows anteroposteriorly (1) toward its medial end. (Upchurch et al., 2004, #285).

431. Posterior margin of medial tip of astragalus, in proximal view: convex or straight (0); concave (1). (NEW).

432. Astragalus, transverse length relatively to the proximodistal height: 50% more than (0) or sub-equal (1). (Wilson, 2002, #214).

433. Ventral surface of the astragalus: flat or slightly concave transversely (0), convex transversely (1). (Upchurch, 1998, #194).

434. Astragalus, posterior fossa shape: undivided (0); divided by a vertical crest (1). (Wilson, 2002, #213).

435. Astragalus, fibular facet: faces laterally (0); faces posterolaterally, anterior margin visible in posterior view (1). (Whitlock, 2011, #186).

436. Astragalus, ascending process length: limited to anterior two-thirds of astragalus (0); extending to posterior margin of astragalus (1). (Wilson and Sereno, 1998, #84).

437. Astragalus, posterior end of proximal face, tubercle: present (0); absent (1) (D'Emic, 2012, #116).

438. Calcaneum: present (0); absent or fails to ossify (1) (McIntosh, 1990, #28).

439. Transverse width of the calcaneum divided by the transverse width of the astragalus: > 0.3 (0); < 0.3 (1). (Upchurch et al., 2007, #265).

440. Distal tarsals 3 and 4: present (0); absent or un-ossified (1). (Wilson, 2002, #216).

441. Metatarsus, posture: bound (0); spreading (1). (Wilson and Sereno, 1998, #52).

442. Metatarsal I proximal condyle, transverse axis orientation relatively to the axis of shaft: perpendicular (0) or angled ventromedially approximately 15° (1). (Wilson, 2002, #218).

443. Metatarsal I distal condyle, transverse axis orientation relatively to the axis of shaft: perpendicular (0) or angled dorsomedially (1). (Wilson, 2002, #219).

444. Metatarsal I distal condyle, posterolateral projection: absent (0); present (1). (Wilson, 2002, #220).

445. Metatarsal I, minimum shaft width relatively to the metatarsals II–IV minimum shaft width: less than (0) or greater (1). (Wilson and Sereno, 1998, #51).

446. Metatarsal I and V proximal condyle size compared to those of metatarsals II and IV: smaller (0) or sub-equal (1). (Wilson and Sereno, 1998, #14).

447. Metatarsal III length compared to the tibia length: more than 30% (0) less than 25% (1). (Wilson and Sereno, 1998, #50).

448. Metatarsals III and IV, minimum transverse shaft diameters to that of metatarsals I or II: sub-equal to (0) or less than 65% (1) (Wilson and Sereno, 1998, #73).

449. Metatarsal IV, proximomedial end, shape: flat or slightly convex (0); possesses a distinct embayment (1) (D'Emic, 2012; #117).

450. Metatarsal IV, distal end, orientation: roughly perpendicular to long axis of bone (0); beveled upwards medially (1). (D'Emic, 2012, #118).

451. Metatarsal V length compared to the length of metatarsal IV: shorter (0) or at least 70% (1). (Wilson and Sereno, 1998, #15).

452. Pedal non-ungual phalanges, shape: longer proximodistally than broad transversely (0); broader transversely than long proximodistally (1). (Wilson and Sereno, 1998, #53).

453. Pedal digits II–IV, penultimate phalanges, development: sub-equal in size to more proximal phalanges (0); rudimentary or absent (1). (Wilson and Sereno, 1998, #55).

454. Pedal unguals, orientation relatively to the digit axis: aligned (0) or lateral deflected (1). (Wilson and Sereno, 1998, #64).

455. Pedal digit I ungual, length relative to pedal digit II ungual: sub-equal (0); 25% larger than that of digit II (1). (Wilson and Sereno, 1998, #16).

456. Pedal digit I ungual, length compared to the metatarsal I: shorter (0) or longer (1). (Wilson and Sereno, 1998, # 54).

457. Pedal ungual I, shape: broader transversely than dorsoventrally (0); sickle-shaped, much deeper dorsoventrally than broad transversely (1). (Wilson and Sereno, 1998, #17).

458. Pedal ungual II–III, shape: broader transversely than dorsoventrally (0); sickle-shaped, much deeper dorsoventrally than broad transversely (1). (Wilson and Sereno, 1998, #56).

459. Pedal digit IV ungual, development: subequal in size to unguals of pedal digits II and III (0); rudimentary or absent (1). (Wilson and Sereno, #57).

460. Unguals of pedal digit II and III, proximal dimensions: as broad as deep (0); significantly broader than deep (1). (Allain and Aquesbi, 2008, #253).

461. Pedal phalanx II-2: square or rectangular in dorsal view (0), reduced in dorsoventrally extent, has an irregular shape, and is a compressed semicircle in dorsal view (1). (Upchurch et al., 2004, # 303).

Others

462. Osteoderms: absent (0); present (1). (Wilson, 2002, #234).

463. Osteoderms shape: bulb and root (0); or scute (1). (NEW, based on Vidal et al., 2014).

464. Posture: bipedal (0); columnar, obligatory quadrupedal posture (1). (Wilson and Sereno, 1998, #1).

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SUPPLEMENTARY MATERIAL 21

Data matrix

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Plateosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Antetonitrus ingenipes	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Vulcanodon karibaensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tazoudasaurus naimi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Barapasaurus tagorei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Shunosaurus lii	0	1	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	?	?
Patagosaurus fariasi	1	?	?	?	1	?	0	0	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cetiosaurus oxoniensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cetiosauriscus stewerti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Omeisaurus	1	1	0	0	1	?	0	0	0	0	1	1	0	1	1	1	0	0	0	0	1	0	?	?	?	0	0	0	?	?
Mamenchisaurus	1	1	1	0	1	?	0	-	0	0	1	1	1	0	1	1	0	0	0	1	1	0	?	?	0	?	0	0	?	?
Chuanjiesaurus anaensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bellusaurus sui	1	?	?	?	?	?	0	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lapparentosaurus madagascariensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Jobaria tiguidensis	1	1	0	0	1	?	0	0	0	0	1	1	1	1	1	?	0	1	0	0	1	0	?	?	0	0	0	0	?	?
Losillasaurus giganteus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Turiasaurus riodevensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	0	0	0	0
Zby atlanticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Haplocanthosaurus priscus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Amazonsaurus maranhensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Zapalasaurus bonapartei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rayosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Histriasaurus boscarollii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rebbachisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Limaysaurus tessonei	?	?	?	?	?	?	?	?	?	?	?	1	?	0	1	?	?	?	?	1	1	1	?	?	0	0	0	0	?	?
Cathartesaura anaerobica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Comahuesaurus windhauseni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Demandasaurus darwini	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nigersaurus taqueti	0	0	2	0	1	?	1	0	1	0	1	1	0	0	?	1	?	?	1	1	1	1	?	?	0	0	0	0	?	?
Dicraeosaurus	0	0	2	1	?	?	?	1	?	?	?	2	?	?	0	1	?	?	?	?	?	?	?	?	?	1	0	0	?	?
Amargasaurus cazaui	?	?	?	?	?	?	?	?	?	?	?	2	?	0	1	1	?	?	?	?	?	?	?	?	?	1	0	0	?	?
Brachytrachelopan mesai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Suuwassea emilieae	0	1	2	1	?	?	?	1	?	?	?	2	?	?	?	?	?	?	?	?	?	1	?	?	0	1	?	?	?	?
Apatosaurus	0	0	2	0	1	?	1	1	1	1	1	2	0	1	1	1	1	?	1	1	1	1	0	0	1	0	1	1	0	0
Tornieria africana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?
Supersaurus vivianae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Barosaurus lentus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kateedocus siberi	0	0	2	0	?	0	0	1	1	1	1	2	0	?	0	?	?	?	?	?	1	1	0	0	1	0	0	1	?	?

Table S.51. Data matrix

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Diplodocus	0	0	2	0	1	0	1	1	1	1	1	2	0	1	1	1	1	1	1	1	1	1	0	0	1	0	1	1	0	0
SHN (JJS) 177	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dinheirosaurus lourinhanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Camarasaurus	1	1	1	0	1	0	0	0	0	0	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Lourinhasaurus alenquerensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
SHN 181	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tehuelchesaurus benetezii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aragosaurus ischiaticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Galveosaurus herreroi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Europasaurus holgeri	1	1	1	0	1	?	0	?	0	0	1	1	1	1	?	0	0	1	0	0	1	0	0	0	0	?	?	?	?	?
Lusotitan atalaiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Brachiosaurus altithorax	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Giraffatitan brancai	1	2	1	0	1	0	0	0	0	0	1	1	1	1	1	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0
Abydosaurus mcintoshi	1	2	?	?	?	?	1	0	0	?	?	1	0	1	0	?	?	1	0	?	1	?	?	?	0	?	?	?	?	?
Venenosaurus dicrocei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sonorasaurus thompsoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cedarosaurus weiskopfae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sauroposeidon proteles	?	?	?	?	1	?	?	?	?	?	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tastavinsaurus sanzi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Huabeisaurus allocotus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Phuwiangosaurus sirindhornae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?
Tangvayosaurus hoffeti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Yunmenglong ruyangensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Qiaowanlong kangxii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euhelopus zdanskyi	0	1	?	0	1	0	0	0	0	1	1	1	?	?	1	1	0	?	?	?	?	?	?	0	?	?	?	?	?	?
Erketu ellisoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Daxiatitan binglingi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chubutisaurus insignis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ligabuesaurus leanzai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Wintonotitan wattsi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Andesaurus delgadoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rukwatitan bisepultus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mendozasaurus neguyelap	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Malawisaurus dixeyi	1	1	2	0	?	?	?	?	?	?	?	1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Argentinosaurus hunculensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dreadnoughtus schrani	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Epachthosaurus sciuttoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rapetosaurus krausei	0	0	2	0	1	?	1	?	1	0	1	2	?	1	0	1	0	?	0	1	?	1	1	1	0	?	0	0	1	1
Muyelensaurus pecheni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Rinconsaurus caudamirus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?
Overosaurus paradasorum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus rionegrinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus maximus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus colhuehuapensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapuiasaurus macedoi	0	0	2	?	1	1	1	?	0	0	1	2	?	1	0	1	0	?	0	1	1	1	1	0	0	?	?	0	1	1
Gondwanatitan faustoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ampelosaurus atacis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
EC1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lirainosaurus astibiae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Diamantinasaurus matildae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Isisaurus colberti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Opisthocoelicaudia skarzynskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Alamosaurus sanjuanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Saltasaurus loricatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?
Neuquensaurus australis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Baurutitan britoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trigonosaurus pricei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Plateosaurus	0	0	0	0	0	0	0	0	1	?	0	0	0	?	0	?	0	0	0	0	0	?	0	0	-	-	?	?	?	?
Antetonitrus ingenipes	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Vulcanodon karibaensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tazoudasaurus naimi	0	0	?	1	0	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?	?	?	0	-	-	?	?	?	?
Barapasaurus tagorei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Shunosaurus lii	0	0	0	0	0	1	0	0	1	0	?	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0
Patagosaurus fariasi	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cetiosaurus oxoniensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cetiosauriscus stewerti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Omeisaurus	?	0	0	1	0	1	0	0	1	0	1	0	0	1	0	0	0	1	0	1	1	0	1	1	?	0	0	0	?	0
Mamenchisaurus	?	0	0	?	0	1	0	0	1	?	0	0	0	0	0	?	0	1	0	?	1	?	1	1	1	0	0	0	0	0
Chuanjiesaurus anaensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bellusaurus sui	?	?	?	?	?	1	0	?	?	?	?	0	?	?	?	?	0	?	?	?	?	?	?	1	1	0	?	?	?	?
Lapparentosaurus madagascariensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Jobaria tiguidensis	1	0	0	1	0	1	0	0	?	?	1	0	0	?	0	0	0	1	0	1	1	0	1	1	1	0	?	?	?	?
Losillasaurus giganteus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Turiasaurus riodevensis	1	0	?	1	?	1	?	0	?	?	?	?	0	?	0	0	0	1	0	1	?	0	?	1	1	0	0	0	?	?
Zby atlanticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Haplocanthosaurus priscus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Amazonsaurus maranhensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Zapalasaurus bonapartei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rayosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Histriasaurus boscarollii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rebbachisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Limaysaurus tessonei	1	1	?	-	0	0	1	1	1	?	1	1	-	?	0	0	1	?	0	-	1	0	1	1	1	0	1	1	0	0
Cathartesaura anaerobica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Comahuesaurus windhauseni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Demandasaurus darwini	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nigersaurus taqueti	1	1	?	-	0	0	1	1	1	0	1	0	-	?	?	1	1	-	-	-	-	0	1	1	1	0	1	1	0	0
Dicraeosaurus	?	0	?	0	1	1	0	0	0	?	1	1	1	?	1	0	0	1	1	1	1	1	1	?	?	?	?	?	?	?
Amargasaurus cazaui	1	0	?	0	1	1	0	0	0	?	1	1	1	?	1	0	0	1	1	1	1	1	?	?	?	?	?	?	?	?
Brachytrachelopan mesai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Suuwassea emilieae	?	?	?	0	0	?	0	0	?	?	?	1	1	?	1	0	0	?	0	?	?	1	?	1	0	?	1	0	?	1
Apatosaurus	?	0	0	1	0	1	0	0	0	0	1	1	1	0	0	1	0	1	0	1	1	0	1	1	0	0	1	0	?	1
Tornieria africana	?	?	?	?	?	1	?	0	?	?	1	1	1	?	?	?	0	?	?	?	?	0	?	?	?	?	?	?	?	?
Supersaurus vivianae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Barosaurus lentus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kateedocus siberi	1	0	0	1	0	1	?	0	1	?	1	1	1	1	1	1	0	1	0	1	1	1	1	1	0	?	1	0	1	1

Table S.51. Data matrix

Taxa	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Diplodocus	1	0	0	1	0	1	0	0	0	0	1	1	1	0	0	1	0	1	0	1	1	0	1	1	0	0	1	0	?	?
SHN (JJS) 177	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dinheirosaurus lourinhanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Camarasaurus	1	0	0	1	0	1	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0	1	1	1	0	0	0	0	0
Lourinhasaurus alenquerensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
SHN 181	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tehuelchesaurus benetezii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aragosaurus ischiaticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Galveosaurus herreroi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Europasaurus holgeri	1	0	?	1	?	0	0	?	0	0	1	0	0	1	1	0	0	1	0	1	1	?	1	1	1	0	0	0	?	?
Lusotitan atalaiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Brachiosaurus altithorax	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Giraffatitan brancai	1	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1	1	0	1	1	1	0	0	0	0	0
Abydosaurus mcintoshi	1	0	?	?	?	1	?	?	?	?	0	0	0	?	?	?	0	1	0	1	1	?	?	?	1	0	?	?	?	?
Venenosaurus dicrocei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sonorasaurus thompsoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cedarosaurus weiskopfae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sauroposeidon proteles	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tastavinsaurus sanzi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Huabeisaurus allocotus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Phuwiangosaurus sirindhornae	1	0	0	1	0	1	?	?	?	1	?	?	?	?	?	?	0	?	?	?	?	?	?	1	1	1	?	?	?	?
Tangvayosaurus hoffeti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Yunmenglong ruyangensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Qiaowanlong kangxii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euhelopus zdanskyi	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	1	1	?	?	?	?	?
Erketu ellisoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Daxiatitan binglingi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chubutisaurus insignis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ligabuesaurus leanzai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Wintonotitan wattsi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Andesaurus delgadoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rukwatitan bisepultus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mendozasaurus neguyelap	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Malawisaurus dixeyi	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Argentinosaurus hunculensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dreadnoughtus schrani	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Epachthosaurus sciuttoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rapetosaurus krausei	?	0	0	0	0	1	?	0	?	1	0	1	1	0	0	?	0	1	0	1	0	?	1	1	1	1	?	?	0	?
Muyelensaurus pecheni	?	?	?	0	?	?	?	?	?	?	0	?	0	?	?	?	0	?	?	?	?	0	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Rinconsaurus caudamirus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Overosaurus paradasorum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus rionegrinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus maximus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus colhuehuapensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapuiasaurus macedoi	1	0	1	1	?	1	0	0	0	?	?	?	?	?	?	?	0	1	0	1	1	?	1	?	1	?	?	?	?	?
Gondwanatitan faustoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ampelosaurus atacis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
EC1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lirainosaurus astibiae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Diamantinasaurus matildae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Isisaurus colberti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Opisthocoelicaudia skarzynskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Alamosaurus sanjuanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Saltasaurus loricatus	?	?	?	1	0	1	0	?	?	1	?	0	1	?	0	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?
Neuquensaurus australis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Baurutitan britoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trigonosaurus pricei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
Plateosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	?	0	0	0	0	?	?	?
Antetonitrus ingenipes	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Vulcanodon karibaensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tazoudasaurus naimi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	?	?	?
Barapasaurus tagorei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Shunosaurus lii	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	1	1	0	0	?	0	0
Patagosaurus fariasi	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
Cetiosaurus oxoniensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cetiosauriscus stewerti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Omeisaurus	?	1	?	?	?	1	1	1	0	0	?	0	?	0	?	?	0	0	?	0	?	0	0	1	1	0	0	0	0	0
Mamenchisaurus	?	0	?	?	?	1	0	1	?	0	0	?	?	?	?	?	?	0	?	0	?	?	?	1	1	0	0	?	?	?
Chuanjiesaurus anaensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bellusaurus sui	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lapparentosaurus madagascariensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Jobaria tiguidensis	?	1	0	?	?	1	1	?	0	0	0	?	?	0	0	?	0	0	?	0	?	0	?	1	1	0	0	0	0	?
Losillasaurus giganteus	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	1	?	0	?	?	?	?	?	1	?	?	?	?	?
Turiasaurus riodevensis	?	?	?	?	?	1	?	?	0	?	?	?	0	0	0	0	1	1	?	?	?	?	?	1	?	?	?	?	?	?
Zby atlanticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Haplocanthosaurus priscus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Amazonsaurus maranhensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Zapalasaurus bonapartei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rayosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Histriasaurus boscarollii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rebbachisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Limaysaurus tessonei	?	2	0	?	?	?	?	?	1	0	0	1	0	1	0	1	0	1	1	0	?	1	0	1	?	?	?	?	?	?
Cathartesaura anaerobica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Comahuesaurus windhauseni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Demandasaurus darwini	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	2	0	?
Nigersaurus taqueti	?	2	?	?	?	?	?	?	1	0	0	1	0	0	0	1	0	?	?	0	?	1	?	1	1	0	1	2	0	?
Dicraeosaurus	1	?	0	?	?	?	1	0	0	0	1	1	1	0	1	0	0	0	1	0	?	1	1	1	1	1	0	1	1	?
Amargasaurus cazaui	?	?	?	?	?	?	?	?	0	0	1	1	1	0	1	0	0	1	?	0	?	1	1	1	?	?	?	?	?	?
Brachytrachelopan mesai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Suuwassea emilieae	?	?	?	?	?	?	?	?	0	?	?	?	?	0	?	0	0	?	?	?	?	?	?	?	?	1	?	1	1	?
Apatosaurus	0	2	0	?	0	1	?	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	?	1	?	0	0	?
Tornieria africana	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	0	?	?	?	?	1	0	?	?	?	?	?	?	?
Supersaurus vivianae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Barosaurus lentus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kateedocus siberi	?	?	?	?	?	?	?	?	0	?	0	1	1	0	0	0	1	0	?	?	?	1	0	1	1	1	0	0	0	?

Table S.51. Data matrix

Taxa	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
Diplodocus	0	2	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	1	1	1	0	0	0	?
SHN (JJS) 177	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dinheirosaurus lourinhanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Camarasaurus	1	1	0	1	?	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0
Lourinhasaurus alenquerensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
SHN 181	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tehuelchesaurus benetezii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aragosaurus ischiaticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Galveosaurus herreroi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Europasaurus holgeri	0	1	0	1	?	?	?	?	0	0	0	0	0	0	0	0	1	1	1	0	?	0	0	1	1	0	0	0	0	?
Lusotitan atalaiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Brachiosaurus altithorax	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Giraffatitan brancai	0	1	0	1	?	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	?	0	0	1	1	0	0	0	0	1
Abydosaurus mcintoshi	0	1	?	0	?	?	?	?	?	0	?	0	?	?	?	?	?	1	0	0	?	0	?	?	0	0	0	?	?	1
Venenosaurus dicrocei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sonorasaurus thompsoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cedarosaurus weiskopfae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sauroposeidon proteles	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tastavinsaurus sanzi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Huabeisaurus allocotus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Phuwiangosaurus sirindhornae	?	?	?	?	?	?	?	?	1	0	0	0	1	1	0	?	1	1	0	0	?	0	?	1	?	?	?	?	?	?
Tangvayosaurus hoffeti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Yunmenglong ruyangensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Qiaowanlong kangxii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euhelopus zdanskyi	?	?	0	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	?	?	?
Erketu ellisoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Daxiatitan binglingi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chubutisaurus insignis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ligabuesaurus leanzai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Wintonotitan wattsi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Andesaurus delgadoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rukwatitan bisepultus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mendozasaurus neguyelap	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Malawisaurus dixeyi	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	1	0	0	?	?	?
Argentinosaurus hunculensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dreadnoughtus schrani	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Epachthosaurus sciuttoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rapetosaurus krausei	2	1	1	1	1	?	?	?	1	1	?	0	1	0	0	?	?	?	1	1	1	0	?	?	1	1	0	1	?	?
Muyelensaurus pecheni	?	?	?	?	?	?	?	?	0	1	?	?	?	?	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
Rinconsaurus caudamirus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Overosaurus paradasorum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus rionegrinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus maximus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus colhuehuapensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapuiasaurus macedoi	?	1	1	1	1	1	?	?	?	1	?	0	0	0	0	?	?	?	1	1	1	0	?	?	1	0	1	?	?	?
Gondwanatitan faustoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ampelosaurus atacis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
EC1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lirainosaurus astibiae	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	1	?	?	0	?	?	?	?	?	?	?	?
Diamantinasaurus matildae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Isisaurus colberti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Opisthocoelicaudia skarzynskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Alamosaurus sanjuanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Saltasaurus loricatus	?	?	?	?	?	?	?	?	0	1	0	0	0	1	0	?	?	1	?	?	?	?	?	1	?	?	?	?	?	?
Neuquensaurus australis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Baurutitan britoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trigonosaurus pricei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Diplodocus	1	1	0	1	1	0	1	?	2	3	1	1	?	1	0	0	1	2	1	0	2	0	3	0	3	0	1	1	?	1
SHN (JJS) 177	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dinheirosaurus lourinhanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1
Camarasaurus	0	1	1	1	1	1	1	1	1	1	1	0	?	0	1	1	0	1	1	0	2	0	0	0	1	0	0	1	0	1
Lourinhasaurus alenquerensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1
SHN 181	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tehuelchesaurus benetezii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aragosaurus ischiaticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Galveosaurus herreroi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1
Europasaurus holgeri	?	1	1	1	1	?	1	1	1	1	1	0	1	0	1	1	0	1	1	0	2	0	1	1	?	?	0	1	0&1	1
Lusotitan atalaiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Brachiosaurus altithorax	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?
Giraffatitan brancai	0	1	1	1	1	1	1	2	1	2	1	0	?	0	0	1	0	1	1	0	2	0	1	1	?	0	0	1	1	1
Abydosaurus mcintoshi	?	1	0	?	?	?	?	2	1	2	1	0	?	0	0	?	2	1	1	?	2	0	?	1	?	?	0	?	?	?
Venenosaurus dicrocei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sonorasaurus thompsoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cedarosaurus weiskopfae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sauroposeidon proteles	?	?	?	?	?	?	?	?	?	0/1/2	?	0	?	0	0	?	0	1	1	?	2	0	1	0	?	?	?	1	1	1
Tastavinsaurus sanzi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Huabeisaurus allocotus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	2	1	?	2	0	1	0	?	?	?	1	1	?
Phuwiangosaurus sirindhornae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	2	1	?	2	0	1	0	?	?	?	1	0	1
Tangvayosaurus hoffeti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Yunmenglong ruyangensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1
Qiaowanlong kangxii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1
Euhelopus zdanskyi	?	1	?	?	?	?	?	?	1	1	1	?	?	1	1	1	0	1	1	?	2	0	0	0	4	?	?	1	1	1
Erketu ellisoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	1
Daxiatitan binglingi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Chubutisaurus insignis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ligabuesaurus leanzai	?	?	?	?	?	?	?	?	?	0/1/2	?	0	?	0	0	1	0	1	1	?	2	0	1	?	?	?	?	1	?	1
Wintonotitan wattsi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Andesaurus delgadoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rukwatitan bisepultus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1
Mendozasaurus neguyelap	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1
Malawisaurus dixeyi	?	?	?	?	?	?	?	?	1	?	1	0	?	?	?	1	?	0	1	?	2	0	1	0	?	?	?	1	0	1
Argentinosaurus hunculensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dreadnoughtus schrani	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1
Epachthosaurus sciuttoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rapetosaurus krausei	0	1	1	?	?	?	?	?	1	2	1	0	?	0	0	1	2	2	1	?	2	0	2	0	4	?	0	1	0	1
Muyelensaurus pecheni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	?	?	?	?	?	?	?	?	?	1	?	?

Table S.51. Data matrix

Taxa	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Diplodocus	1	1	0	1	1	0	1	?	2	3	1	1	?	1	0	0	1	2	1	0	2	0	3	0	3	0	1	1	?	1
SHN (JJS) 177	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dinheirosaurus lourinhanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1
Camarasaurus	0	1	1	1	1	1	1	1	1	1	1	0	?	0	1	1	0	1	1	0	2	0	0	0	1	0	0	1	0	1
Lourinhasaurus alenquerensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1
SHN 181	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tehuelchesaurus benetezii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aragosaurus ischiaticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Galveosaurus herreroi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1
Europasaurus holgeri	?	1	1	1	1	?	1	1	1	1	1	0	1	0	1	1	0	1	1	0	2	0	1	1	?	?	0	1	0&1	1
Lusotitan atalaiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Brachiosaurus altithorax	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?
Giraffatitan brancai	0	1	1	1	1	1	1	2	1	2	1	0	?	0	0	1	0	1	1	0	2	0	1	1	?	0	0	1	1	1
Abydosaurus mcintoshi	?	1	0	?	?	?	?	2	1	2	1	0	?	0	0	?	2	1	1	?	2	0	?	1	?	?	0	?	?	?
Venenosaurus dicrocei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sonorasaurus thompsoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cedarosaurus weiskopfae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sauroposeidon proteles	?	?	?	?	?	?	?	?	?	0/1/2	?	0	?	0	0	?	0	1	1	?	2	0	1	0	?	?	?	1	1	1
Tastavinsaurus sanzi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Huabeisaurus allocotus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	2	1	?	2	0	1	0	?	?	?	1	1	?
Phuwiangosaurus sirindhornae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	2	1	?	2	0	1	0	?	?	?	1	0	1
Tangvayosaurus hoffeti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Yunmenglong ruyangensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1
Qiaowanlong kangxii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1
Euhelopus zdanskyi	?	1	?	?	?	?	?	?	1	1	1	?	?	1	1	1	0	1	1	?	2	0	0	0	4	?	?	1	1	1
Erketu ellisoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	1
Daxiatitan binglingi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Chubutisaurus insignis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ligabuesaurus leanzai	?	?	?	?	?	?	?	?	?	0/1/2	?	0	?	0	0	1	0	1	1	?	2	0	1	?	?	?	?	1	?	1
Wintonotitan wattsi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Andesaurus delgadoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rukwatitan bisepultus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1
Mendozasaurus neguyelap	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1
Malawisaurus dixeyi	?	?	?	?	?	?	?	?	1	?	1	0	?	?	?	1	?	0	1	?	2	0	1	0	?	?	?	1	0	1
Argentinosaurus huncullensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dreadnoughtus schrani	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1
Epachthosaurus sciuttoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rapetosaurus krausei	0	1	1	?	?	?	?	?	1	2	1	0	?	0	0	1	2	2	1	?	2	0	2	0	4	?	0	1	0	1
Muyelensaurus pecheni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	?	?	?	?	?	?	?	?	?	1	?	?

Table S.51. Data matrix

Taxa	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Rinconsaurus caudamirus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	2	0	?	?	?	?	?	1	?	?
Overosaurus paradasorum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1
Aelosaurus rionegrinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus maximus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus colhuehuapensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapuiasaurus macedoi	?	?	0	?	?	1	?	?	1	2	1	0	?	0	0	1	2	2	1	0	2	0	2	0	?	?	?	1	?	?
Gondwanatitan faustoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ampelosaurus atacis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	1	0	1
EC1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1
Lirainosaurus astibiae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	1	0	2	0	2	0	?	?	?	?	?	?
Diamantinasaurus matildae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Isisaurus colberti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?
Opisthocoelicaudia skarzynskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Alamosaurus sanjuanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	2	1	?	2	0	1	?	?	?	?	1	?	1
Saltasaurus loricatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1
Neuquensaurus australis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1
Baurutitan britoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trigonosaurus pricei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1

Table S.51. Data matrix

Taxa	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150
Plateosaurus	1	1	?	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0	0	0	0	?	0	0	0	0	0	-	?
Antetonitrus ingenipes	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	0	-	?
Vulcanodon karibaensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tazoudasaurus naimi	0	1	?	0	0	?	?	?	?	?	?	?	?	?	0	0	?	?	0	0	0	1	0	0	0	0	?	1	0	?
Barapasaurus tagorei	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	?	?	?	?	-	?
Shunosaurus lii	0	1	0	0	0	0	0	0	1	0	?	?	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	-	0
Patagosaurus fariasi	0	0	?	2	0	?	0	?	1	0	1	1	0	0	0	0	?	?	0	0	0	1	0	1	1	0	1	0	-	?
Cetiosaurus oxoniensis	2	0	?	0	0	?	?	?	?	?	?	?	?	?	0	0	?	?	0	0	0	1	0	1	1	0	1	0	-	?
Cetiosauriscus stewerti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Omeisaurus	0	0	?	1&2	0	0	0	0	?	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	-	0
Mamenchisaurus	1&2	0	0	2	0	0	0	0	1	0	1	1	?	0	0	0	?	0	0	0	1	0	1	1	0	0	1	1	0	0
Chuanjiesaurus anaensis	?	0	?	2	0	0	0	0	1	?	?	?	?	?	?	?	?	0	?	?	?	0&1	1	?	?	?	?	?	?	0
Bellusaurus sui	2	0	?	1	?	?	?	0	?	?	?	?	?	?	0	0	?	?	0	0	0	1	0	1	1	0	1	?	-	?
Lapparentosaurus madagascariensis	1	?	0	0	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Jobaria tiguidensis	1	0	?	0	1	0	0	0	?	0	?	1	0	1	0	0	0	?	0	0	0	1	0	0	1	0	1	0	-	0
Losillasaurus giganteus	1	0	?	0	?	0	?	?	?	?	1	1	0	?	0	0	?	0	0	0	0	1	0	1	1	0	?	0	-	?
Turiasaurus riodevensis	1	0	?	0	1	0	0	0	1	?	1	1	?	?	0	?	1	0	0	0	0	1	0	1	?	0	1	1	0	?
Zby atlanticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Haplocanthosaurus priscus	1	0	?	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	-	0
Amazonsaurus maranhensis	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Zapalasaurus bonapartei	1	0	?	?	?	?	?	?	?	?	?	?	2	?	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?
Rayosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Histriasaurus boscarollii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rebbachisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Limaysaurus tessonei	1	0	?	1	?	0	?	?	?	?	?	?	2	?	0	0	?	0	0	0	0	1	0	0	0	0	1	0	-	0
Cathartesaura anaerobica	1	0	?	1	?	0	?	?	?	0	?	?	2	?	?	?	?	?	?	0	?	?	?	0	0	0	1	0	-	?
Comahuesaurus windhauseni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Demandasaurus darwini	1	0	?	1	?	?	0	?	?	?	?	?	2	?	0	0	?	?	0	0	0	1	0	2	0	0	1	0	-	?
Nigersaurus taqueti	1	0	1	1	1	0	?	1	1	?	1	1	2	0	0	0	?	0	0	0	0	1	0	2	0	0	1	0	-	0
Dicraeosaurus	1	0	?	0	0	0	0	0	1	0	1	0	0	0	-	1	1	1	-	-	1	1	0	1	1	0	1	1	1	1
Amargasaurus cazaui	1	0	?	?	0	0	?	?	?	0	1	0	0	?	-	1	1	1	-	-	1	1	0	1	0	0	1	1	0	1
Brachytrachelopan mesai	1	?	?	0	?	0	?	?	?	?	?	?	0	?	?	1	1	1	?	-	?	?	?	?	?	?	?	?	?	?
Suuwassea emilieae	1	0	?	1	1	0	0	0	?	?	1	1	0	1	0	0	1	1	-	1	?	?	0	1	0	?	?	0	?	0
Apatosaurus	1	0	1	2	1	0	0	1	1	0	1	0	0	0	0	1	1	1	-	-	1	1	0	2	1	0	1	1	1	0
Tornieria africana	1	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?
Supersaurus vivianae	?	0	?	?	?	0	?	?	?	?	?	?	0	1	?	1	?	0	?	?	?	?	?	?	?	1	?	1	?	0
Barosaurus lentus	1	0	?	?	1	0&1	0	0	?	0	1	?	0	1	0	1	1	0	-	-	1	1	1	2	0	1	1	1	1	0
Kateedocus siberi	1	0	1	?	?	0	0	0	1	0	1	1	0	1	1	0	1	0	-	-	1	1	1	2	0	1	1	1	1	0

Table S.51. Data matrix

Taxa	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150
Diplodocus	?	0	1	2	1	1	0	0	1	0	1	0	0	1	0	1	1	0	-	-	0	1	1	2	1	1	1	1	1	0
SHN (JJS) 177	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dinheirosaurus lourinhanensis	?	0	1	?	1	1	0	0	?	0	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?
Camarasaurus	2	0	1	1	1	0	0	0	1	0	1	0	0	0	0	1	1	0	-	0	0	1	0	1	1	0	1	1	1	0
Lourinhasaurus alenquerensis	2	0	?	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
SHN 181	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tehuelchesaurus benetezii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aragosaurus ischiaticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Galveosaurus herreroi	0	0	1	2	1	0	0	0	?	0	?	?	0	0	?	?	?	?	?	1	?	?	1	?	?	0	?	?	?	?
Europasaurus holgeri	2	0	1	1	1	?	0	0	1	0	1	0	0	0	1	0	0	?	0	1	0	1	0	1	1	0	1	0	-	0
Lusotitan atalaiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Brachiosaurus altithorax	2	0	?	2	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	0	1	1	1	?	?	?	1	?	?	?
Giraffatitan brancai	2	0	1	2	1	0	0	0	1	?	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	0	-	0
Abydosaurus mcintoshi	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?
Venenosaurus dicrocei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sonorasaurus thompsoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cedarosaurus weiskopfae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?
Sauroposeidon proteles	2	0	1	2	1	0	0	0	?	?	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	-	0
Tastavinsaurus sanzi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Huabeisaurus allocotus	1	0	?	?	0	?	0	1	?	0	?	?	1	?	?	?	?	?	0	?	0	?	0	0	?	0	1	1	?	?
Phuwiangosaurus sirindhornae	3	0	1	?	1	0	0	0	1	0	1	1	1	1	0	1	1	0	0	?	0	1	1	1	0	0	1	1	0	0
Tangvayosaurus hoffeti	?	?	?	?	?	?	?	?	?	0	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Yunmenglong ruyangensis	?	0	?	2	?	?	?	1	1	?	1	1	1	1	?	1	1	?	?	?	0	1	0	0	?	?	?	?	?	0
Qiaowanlong kangxii	3	0	1	?	?	?	0	0	?	0	1	1	1	1	?	1	1	0	0	?	0	1	0	0	?	?	1	1	0	0
Euhelopus zdanskyi	0	0	0	2	0	0	0	1	1	0	1	1	1	1	0	0	1	0	0	0	0	1	1	?	1	?	1	1	1	0
Erketu ellisoni	1	0	1	2	?	0	0	1	1	?	1	1	1	1	0	1	1	0	0	0	0	1	1	0	1	0	1	1	?	?
Daxiatitan binglingi	?	0	0	?	0	0	0	1	?	0	1	1	1	1	?	?	1	0	?	?	0	?	?	?	?	?	?	?	?	0
Chubutisaurus insignis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ligabuesaurus leanzai	3	0	1	2	0	?	0	0	?	1	?	?	0	?	?	?	?	?	1	0	?	?	?	0	0	0	1	0	-	?
Wintonotitan wattsi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Andesaurus delgadoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rukwatitan bisepultus	3	1	0	2	0	0	1	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	?	?	?
Mendozasaurus neguyelap	?	?	?	2	?	0	?	?	?	?	0	-	0	?	?	?	?	?	1	0	?	1	?	0	0	0	1	0	-	?
Malawisaurus dixeyi	3	1	1	?	0	0	1	0	1	1	0	-	0	0	1	0	0	0	0	1	0	1	0	1	0	?	0	1	0	-	0
Argentinosaurus hunculensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dreadnoughtus schrani	3	0	0	2	0	0	1	0	?	?	0	-	0	0	?	?	?	0	?	0	0	1	1	0	0	0	?	?	-	0
Epachthosaurus sciuttoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rapetosaurus krausei	3	1	0	2	0	0	1	0	1	1	?	?	0	?	1	0	0	?	0	1	0	1	1	0	1	0	1	0	-	0
Muyelensaurus pecheni	?	0	?	2	0	0	1	0	?	?	0	-	?	0	?	?	?	0	?	?	0	1	1	?	?	?	?	0	-	0

Table S.51. Data matrix

Taxa	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150
Rinconsaurus caudamirus	?	0	?	?	?	?	?	?	?	1	?	?	?	?	?	0	?	?	?	?	?	1	?	1	?	?	1	0	-	?
Overosaurus paradasorum	?	0	?	2	0	0	1	0	?	1	0	-	0	0	?	?	?	0	0	?	?	?	1	0	1	0	1	0	-	0
Aelosaurus rionegrinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus maximus	?	0	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
Aelosaurus colhuehuapensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapuiasaurus macedoi	?	0	?	2	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	1	1	?	?	?	?	?	?	?
Gondwanatitan faustoi	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ampelosaurus atacis	3	?	?	2	?	?	?	?	?	1	?	?	?	?	?	?	?	?	0	1	?	?	?	0	1	?	?	0	-	?
EC1	3	0	0	2	0	0	?	0	1	?	0	-	0	0	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
Lirainosaurus astibiae	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Diamantinasaurus matildae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Isisaurus colberti	3	1	?	2	0	0	1	0	0	1	0	-	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	-	1
Opisthocoelicaudia skarzynskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Alamosaurus sanjuanensis	3	1	0	2	0	0	1	0	?	1	0	-	0	0	0	0	0	0	0	0	?	0	0	0	0	0	1	0	-	0
Saltasaurus loricatus	3	0	0	2	0	0	1	0	0	1	0	-	0	0	0	0	0	?	0	1	0	1	0	0	0	0	1	0	-	0
Neuquensaurus australis	3	0	?	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?	?	0	0	0	1	0	-	?
Baurutitan britoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trigonosaurus pricei	3	1	?	2	0	0	1	0	?	1	0	-	0	0	0	?	0	0	0	0	0	1	1	0	0	0	1	0	-	0

Table S.51. Data matrix

Taxa	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180
Plateosaurus	0	?	?	?	?	?	?	?	?	0	?	0	?	0	0	-	?	0	0	0	0	0	0	0	-	1	-	0	0	0
Antetonitrus ingenipes	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	-	?	0	0	0	0	0	1	1	2	1	-	0	0	0
Vulcanodon karibaensis	?	?	?	?	?	?	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tazoudasaurus naimi	0	?	?	?	?	?	?	1	?	?	?	?	?	?	0	-	?	0	0	0	0	1	1	0	-	0	0	0	0	0
Barapasaurus tagorei	0	?	?	?	?	?	?	?	?	0	?	?	?	?	0	-	?	0	0	0	0	1	1	?	?	0	?	1	?	?
Shunosaurus lii	1	0	0	0	0	0	-	?	0	?	0	0	0	1	0	-	?	1	0	0	0	1	1	0	-	1	-	1	0	0
Patagosaurus fariasi	0	?	?	0	?	0	-	0	?	0	0	?	?	?	1	0	0	1	0	0	0	1	1	0	-	0	0	1	0	0
Cetiosaurus oxoniensis	0	?	?	?	?	?	?	?	?	0	?	?	1	?	1	?	0	1	0	0	0	1	1	0	-	0	0	1	0	?
Cetiosauriscus stewerti	?	?	?	?	?	?	?	?	?	0	?	?	?	?	1	0	0	?	?	?	0	?	?	?	?	?	?	?	?	?
Omeisaurus	1	0	?	?	0	0	-	1	0	?	0	0	1	2	1	0	0	0	0	0	1&2	1	1	1	0	0	1	1	0	0
Mamenchisaurus	0	?	?	0	0	0	0	1	0	1	0	0	1	2	1	0	0	0	0	1	2	1	1	1	0	0	1	1	1	1
Chuanjiesaurus anaensis	?	0	?	0	?	?	-	1	0	1	?	0	?	?	1	0	0	0	0	?	?	?	1	1	?	?	?	1	?	?
Bellusaurus sui	?	?	?	?	?	?	?	0	?	?	?	1	?	?	1	?	?	0	0	1	1	1	1	1	1	0	1	1	1	1
Lapparentosaurus madagascariensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	-	0	?	0	0/1	0	1	1	1	0	0	1	?	?	1
Jobaria tiguidensis	0	0	0	0	0	1	?	0	?	1	?	0	1	2	0	-	?	1	0	1	0	1	1	0	-	0	0&1	1	1	1
Losillasaurus giganteus	?	?	?	?	?	?	?	0	?	?	?	?	?	?	1	0	0	1	1	1	0	1	1	1	0	0	1	1	1	0
Turiasaurus riodevensis	1	?	?	?	?	?	0	0	?	1	?	0	1	?	1	0	0	1	0&1	1	0	1	1	1	0	0	0	1	?	0
Zby atlanticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Haplocanthosaurus priscus	0	0	0	0	0	0	-	0	0	1	0	1	1	0	1	0	0	1	1	1	0	1	1	1	0	0	1	1	1	1
Amazonsaurus maranhensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	1	1	1	?	?	?	?	1	?	?
Zapalasaurus bonapartei	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rayosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Histriasaurus boscarollii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	0	1	?	?	?	?	?	?	?	?	?	1
Rebbachisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	0	1	?	1	1	0	-	0	2	?	?	?
Limaysaurus tessonei	?	?	0	0	0	0	?	?	?	?	?	1	?	?	1	?	?	1	?	1	1	?	?	0	-	0	2	1	1	1
Cathartesaura anaerobica	?	?	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Comahuesaurus windhauseni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	1	0	1	1	1	1	0	-	0	?	1	2	2
Demandasaurus darwini	?	?	?	?	?	0	?	?	?	?	?	1	1	?	1	0	1	1	?	?	1	?	1	0	-	0	2	?	?	?
Nigersaurus taqueti	?	0	0	0	0	0	-	0	0	1	?	1	?	2	1	0	1	1	?	1	1	1	1	0	-	0	2	1	?	2
Dicraeosaurus	1	1	0	0	0	?	1	0	0	0	0	1	1	2	0	-	-	1	0	2	0	1	1	0	-	1	-	1	1	1
Amargasaurus cazaui	0	1	0	0	?	0	1	0	?	0	?	1	?	?	0	-	-	1	0	2	0	1	1	0	-	1	-	1	1	1
Brachytrachelopan mesai	?	1	0	?	?	?	1	?	?	?	?	1	?	2	0	-	-	1	0	2	0	1	1	0	-	1	-	1	1	?
Suuwassea emilieae	0	?	?	?	0	?	1	0	?	0	?	1	1	?	1	0	?	1	0	?	1	1	1	?	?	?	?	?	1	2	?
Apatosaurus	0	0&1	0	0	1	0	0	0	0	1	0	1	1	4	1	0	1	0	0	0	1	1	1	0	-	0	2	1	1	1
Tornieria africana	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Supersaurus vivianae	?	1	0	?	1	?	0	?	?	?	?	?	?	?	1	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?
Barosaurus lentus	1	0	1	1	0	1	0	0	?	?	1	1	1	4	1	0	?	0	0	0	1	1	1	0	-	0	2	1	1	1
Kateedocus siberi	1	0	0	1	1	0	1	?	?	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

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Taxa	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180
Diplodocus	1	0	1	1	0	1	0	0	0	1	1	1	1	4	1	0	1	0	0	0	1	1	1	?	?	0	?	1	1	1
SHN (JJS) 177	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dinheirosaurus lourinhanensis	?	1	1	1	1	1	?	?	?	?	?	?	?	?	1	0	1	?	0	?	1	?	?	?	?	?	?	1	1	1
Camarasaurus	0	0	0	0	1	0	0	0	0	0	0	0	1	2	1	0	1	0	0	1	1	1	1	0	-	0	0	1	1	1
Lourinhasaurus alenquerensis	?	?	?	?	1	?	?	?	?	?	?	?	?	?	1	0	1	?	?	1	1	?	?	?	?	?	?	1	?	?
SHN 181	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tehuelchesaurus benetezii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	0	0	1	1	1	0	-	0	0	1	2	1
Aragosaurus ischiaticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Galveosaurus herreroi	?	?	?	?	0	?	?	?	?	?	?	0	1	?	1	0	1	0	?	1	1	1	1	1	1	0	1	?	?	1
Europasaurus holgeri	0	0	0	0	0	0	-	0	?	0	0	0	1	?	1	0	1	0	0	1	1	1	1	1	1	0	1	1	2	1
Lusotitan atalaiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	?	?	?	1	?	?	?	?	?	?	?	?	?
Brachiosaurus altithorax	?	?	?	?	?	?	?	?	?	?	0	?	?	?	1	0	1	0	0	1	1	1	1	1	0	0	1	1	0	0
Giraffatitan brancai	0	0	0	0	1	0	-	0	1	0	?	0	1	2	1	0	1	0	0	1	1	1	1	1	0	0	1	1	1	0
Abydosaurus mcintoshi	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Venenosaurus dicrocei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sonorasaurus thompsoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	?	?	?	2	?	?	?	?	?	?	?	?	?
Cedarosaurus weiskopfae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	0	1	2	?	?	?	?	?	?	?	?	?
Sauroposeidon proteles	0	?	?	?	?	?	?	0	1	1	?	?	1	?	1	0	1	1	0	0	2	1	1	1	0&1	?	?	1	1	1
Tastavinsaurus sanzi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	0	1	1	1	1	1	0	0	?	?	1	?
Huabeisaurus allocotus	?	?	?	0	?	0	?	?	?	1	0	?	1	?	1	0	?	0	0	?	2	1	1	1	1	?	?	1	?	?
Phuwiangosaurus sirindhornae	0	?	?	0	?	0	0	0	0	1	0	1	1	2	1	0	1	0&1	0	1	2	1	1	1	1	0	0	1	1	1
Tangvayosaurus hoffeti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0&1	?	?	?	?	?	?	?	?	?	?	?	?	?
Yunmenglong ruyangensis	0	?	?	?	?	?	?	1	?	?	?	0	?	?	1	0	?	?	?	1	2	?	?	?	?	?	?	?	?	?
Qiaowanlong kangxii	0	?	?	?	?	?	?	1	0	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euhelopus zdanskyi	1	?	?	0	?	0	0	1	0	?	0	0	1	1	1	1	0	1	0	1	2	1	0	1	1	0	1	1	1	1
Erketu ellisoni	?	?	?	?	?	?	?	1	1	1	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Daxiatitan binglingi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	1	?	?	?	?	?	?	?	?	?	1	?	?
Chubutisaurus insignis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	2	?	1	0	-	0	0	1	?	1
Ligabuesaurus leanzai	?	0	?	?	0	?	-	?	?	?	?	?	?	?	1	1	0	0	0	1	2	1	0	1	1	1	-	1	1	1
Wintonotitan wattsi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	2	?	?	?	?	?	?	?	?	?
Andesaurus delgadoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	1	2	?	1	?	-	1	-	?	1	1
Rukwatitan bisepultus	?	?	?	0	?	?	?	?	?	1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mendozasaurus neguyelap	?	?	?	?	?	?	-	?	?	?	0	?	?	?	1	1	0	0	?	0	2	1	?	1	2	1	-	1	2	2
Malawisaurus dixeyi	0	?	?	0	?	0	?	0	0	1	0	0	?	?	1	1	0	1	0	1	2	1	1	1	2	1	-	1	2	2
Argentinosaurus hunculensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	0	0	1	2	0	?	1	2	1	-	1	2	1
Dreadnoughtus schrani	0	?	0	?	?	?	?	0	?	?	?	?	?	?	1	1	0	0	0	1	2	0&1	1	1	2	1	-	1	2	1
Epachthosaurus sciuttoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	1	2	0	1	1	2	1	-	1	?	1
Rapetosaurus krausei	0	?	?	0	?	0	-	0	0	0	0	?	?	?	1	1	?	0	0	0	2	0&1	0	1	2	1	-	1	2	2
Muyelensaurus pecheni	?	?	?	?	?	?	?	0	?	?	?	1	1	?	1	0	?	0	1	0	?	0	0	1	2	1	-	1	?	2

Table S.51. Data matrix

Taxa	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180
Rinconsaurus caudamirus	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	1	?	0	1	?	?	?	?	1	2	?	?	?	2	1
Overosaurus paradasorum	0	?	?	0	?	0	-	?	?	?	0	?	1	4	1	1	0	?	?	?	2	0	0	1	2	1	-	1	2	?
Aelosaurus rionegrinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus maximus	1	?	?	?	?	?	?	?	?	0	?	0	?	?	?	?	?	0	0	?	2	?	?	?	?	?	?	?	?	?
Aelosaurus colhuehuapensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapuiasaurus macedoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	0	0	0&1	2	0	?	1	2	1	-	1	1	2
Gondwanatitan faustoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	1	2	?	?	1	2	2
Ampelosaurus atacis	?	?	?	?	?	?	-	?	?	?	?	?	?	?	1	1	0	0	?	1	2	?	?	1	?	?	?	1	2	?
EC1	?	?	?	?	?	?	?	0	?	?	?	?	1	?	1	1	0	0	?	1	2	0	?	?	?	?	?	1	2	2
Lirainosaurus astibiae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	1	1	1	2	?	0	1	2	1	-	1	?	2
Diamantinasaurus matildae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	?	1	2	?	?	1	2	1	-	?	?	?
Isisaurus colberti	?	0	?	0	0	0	-	0	?	0	0	?	1	?	1	1	?	0	0	0	2	0	0	1	2	1	-	1	1	2
Opisthocoelicaudia skarzynskii	?	?	?	?	?	?	?	?	?	?	?	?	?	4	1	1	?	0	0	1	2	0	0	1	2	1	-	1	2	2
Alamosaurus sanjuanensis	?	?	0	?	?	?	-	0	?	?	0	?	1	?	1	1	0	0&1	1	1	1&2	1	0	1	2	1	-	1	1	2
Saltasaurus loricatus	0	?	?	0	?	0	-	0	?	0	0	?	?	?	1	1	0	1	1	1	2	0	0	1	2	1	-	1	2	2
Neuquensaurus australis	0	?	?	?	?	?	-	?	?	0	?	?	?	?	1	1	?	1	1	1	2	0	0	1	2	1	-	1	2	2
Baurutitan britoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trigonosaurus pricei	1	?	0	0	0	0	-	0	?	0	0	?	?	4	1	1	?	1	1	1	2	1	0	1	2	1	-	1	2	2

Table S.51. Data matrix

Taxa	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210
Plateosaurus	0	0	0	?	0	0	0	0	0	0	0	0	0	?	0	0	0	-	-	0	0	-	-	0	0	?	?	0	0	0
Antetonitrus ingenipes	0	0	0	?	0	0	0	0	0	0	0	0	0	?	0	0	0	-	-	0	1	-	-	0	0	?	?	0	0	0
Vulcanodon karibaensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tazoudasaurus naimi	0	0	0	?	1	0	0	0	0	0	1	1	0	?	0	0	1	0	0	1	1	1	?	0	0	?	?	0	0	1
Barapasaurus tagorei	1	0	1	?	0	0	0	0	?	0	1	1	1	?	0	0	1	0	0	1	1	1	?	0	0	?	?	0	0	1
Shunosaurus lii	0	0	0	0	0	0	0	0	0	0	1	1	1	-	0	1	0&1	0	-	1	1	0&1	?	0	0	0	?	0	0	1
Patagosaurus fariasi	0	0	0	?	1	0	1	0	0	0	1	1	0	?	0	1	0	-	-	1	1	-	-	0	0	0	?	0	0	1
Cetiosaurus oxoniensis	2	0	0	0	0	0	1	0	0	?	1	1	0	?	1	1	0	-	-	1	1	-	-	0	0	0	0	0	0	0&1
Cetiosauriscus stewerti	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?
Omeisaurus	0	0	0	?	0	0	1	0	0	?	1	1	1	?	1	0	1	0	0	1	1	1	?	0	0	0	?	0	2	1
Mamenchisaurus	0	0	1	0	0	0	1	0	0	0	1	1	0	-	0	2	1	0	0	1	?	1	1	0	0	0	0	0	2	1
Chuanjiesaurus anaensis	?	?	1	?	?	?	?	?	?	?	1	1	?	?	?	?	1	0	?	?	1	1	1	0	?	?	?	0	2	?
Bellusaurus sui	0	0	0	?	0	0	1	0	0	0	?	1	0	-	1	1	1	0	0	1	1	1	1	0	0	0	?	0	2	1
Lapparentosaurus madagascariensis	0	0	0	0	1	?	1	0	0	0	1	1	1	0	0	1	1	0	0	1	1	0	-	0	0	0	0	?	0	0
Jobaria tiguidensis	0	0	0	0	0	0	1	0	0	0	?	1	1	0	?	1	1	0	0	1	1	1	?	0	0	?	0	0	0	0
Losillasaurus giganteus	0	0	1	0	0	0	1	0	0	0	1	1	1	0	0	1	1	0	0	1	1	1	1	1	0	0	1	0	1	1
Turiasaurus riodevensis	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	1	1	0	0	1	1	1	0	?	?	?	1	?	1	1
Zby atlanticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Haplocanthosaurus priscus	0	0	0	?	0	1	1	0	0	0	1	1	0	-	0	1	1	0	0	1	1	1	0	1	0	0	?	?	1	1
Amazonsaurus maranhensis	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	?	0	1	1	1	?	?	1	?	?	?	?	?
Zapalasaurus bonapartei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rayosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Histriasaurus boscarollii	0	?	0	?	0	1	?	?	0	0	?	?	?	?	0	0	1	0	1	1	1	1	?	0	1	2	?	?	0	1
Rebbachisaurus	0	1	2	?	0	1	1	1	0	0	1	1	1	?	0	0	1	0	1	1	1	1	?	1	1	2	?	1	0	1
Limaysaurus tessonei	0	?	2	?	0	1	1	1	0	0	1	1	0	?	0	0	1	0	1	1	1	1	?	?	1	2	0	1	0	1
Cathartesaura anaerobica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Comahuesaurus windhauseni	0	?	?	?	?	?	?	?	?	0	?	?	?	?	0	0	1	1	1	1	1	1	?	?	1	2	?	?	0	1
Demandasaurus darwini	0	1	1	0	0	?	?	1	0	1	1	1	1	?	0	0	1	0	1	?	1	1	?	?	1	2	?	?	0	1
Nigersaurus taqueti	0	1	1	0	1	1	1	1	0	1	1	1	1	0	0	?	1	0	1	1	1	1	?	1	1	2	?	0	0	1
Dicraeosaurus	0	0	0	0	0	1	1	1	0	1	1	0	0	-	0	0	1	0	0	1	1	1	?	1	0	-	0	0	0	1
Amargasaurus cazaui	0	0	2	0	0	1	1	1	0	?	1	0	?	?	0	0	1	0	0	1	1	1	?	0	0	-	?	0	0	1
Brachytrachelopan mesai	0	1	0	0	0	1	1	1	0	1	1	0	0	-	0	0	1	0	0	1	1	1	?	1	0	-	?	0	0	1
Suuwassea emilieae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?
Apatosaurus	0	0	0	1	1	0	1	0	0	1	1	1	1	0	0	0	1	0	0	1	1	1	?	0	1	2	0	0	0	1
Tornieria africana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Supersaurus vivianae	?	0	0	1	?	?	?	0	0	1	?	1	1	0	0	0	1	?	0	?	1	?	?	0	?	?	0	?	0	1
Barosaurus lentus	0	0	0	1	1	0	1	0	0	1	1	1	1	1	0	0	1	0	0	1	1	1	?	0	1	2	0	0	0	1
Kateedocus siberi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210
Diplodocus	0	0	?	1	1	0	1	0	0	1	1	1	1	1	0	0	1	0	0	1	1	1	?	0	1	2	0	0	1	1
SHN (JJS) 177	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dinheirosaurus lourinhanensis	0	0	?	1	?	0	?	0	0	1	1	1	1	0	0	0	1	?	0	?	?	1	-	0	?	?	?	0	?	?
Camarasaurus	0	0	0	0	0	0	1	0	0	0	1	1	0	-	1	2	1	0	0	1	1	1	1	0	0	0	1	0	2	1
Lourinhasaurus alenquerensis	0	?	?	?	?	?	1	?	?	?	1	1	0	-	1	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?
SHN 181	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tehuelchesaurus benetezii	0	0	1	?	1	0	1	0	0	0	1	0	0	-	?	0	1	0	0	1	1	1	-	0	0	?	?	0	2	0
Aragosaurus ischiaticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Galveosaurus herreroi	0	0	?	?	0	?	?	0	0	0	1	1	0	-	1	1	1	0	0	?	1	1	0	1	?	?	0	?	?	?
Europasaurus holgeri	0	0	0	0	0	1	1	0	0	0	1	1	0	-	0	1	1	0	0	1	1	1	1	1	0	1	0	0	2	1
Lusotitan atalaiensis	0	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
Brachiosaurus altithorax	0	0	0	0	0	1	1	0	0	?	1	1	1	1	1	2	1	0	0	1	1	1	0	0	1	1	0	0	1	1
Giraffatitan brancai	0&2	0	0	0	0	1	1	0	0	0	1	1	1	1	1	2	1	0	0	1	1	1	0	0	1	1	1	0	2	1
Abydosaurus mcintoshi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Venenosaurus dicrocei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sonorasaurus thompsoni	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?
Cedarosaurus weiskopfae	?	?	?	?	?	0	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	2	?
Sauroposeidon proteles	?	0	0	?	0	0	1	0	0	0	1	1	1	?	1	1	1	0&1	0	1	1	1	?	0	0	1	0	0	2	1
Tastavinsaurus sanzi	0	0	0	?	0	?	1	0	0	0	1	1	0	-	1	1	1	0	0	?	1	0	-	0	0	0	0	0	2	1
Huabeisaurus allocotus	0	?	?	?	1	?	1	0	1	?	1	?	1	?	0&1	1	1	0	0	?	?	?	?	0	?	?	?	?	2	1
Phuwiangosaurus sirindhornae	1	0	1	?	0	0	?	0	1	0	1	1	1	?	1	2	1	0&1	0	1	1	1	1	0	0	1	0	1	2	1
Tangvayosaurus hoffeti	?	0	?	?	?	?	?	?	?	0	1	?	1	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	2	?
Yunmenglong ruyangensis	?	0	1	?	0	?	?	0	0	0	1	1	1	?	1	1	1	0	0	?	?	?	?	0	0	?	?	1	2	1
Qiaowanlong kangxii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euhelopus zdanskyi	0	0	?	?	?	?	1	0	0&1	?	1	1	1	0	0	1	1	1	0	1	1	1	1	0	0	?	?	0	2	1
Erketu ellisoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Daxiatitan binglingi	?	0	?	?	?	?	?	0	1	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	2	?
Chubutisaurus insignis	1	0	?	?	0	?	1	?	1	0	?	?	?	?	1	?	1	0	?	?	1	0	-	0	0	?	?	?	2	1
Ligabuesaurus leanzai	1	0	0	?	0	0	1	0	1	?	1	1	1	1	1	1	1	0	0	1	1	1	1	0	0	1	?	0	2	1
Wintonotitan wattsi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Andesaurus delgadoi	?	0	0	?	0	?	1	0	1	?	1	1	1	?	?	1	1	0	0	1	1	1	1	0	0	1	?	0	2	1
Rukwatitan bisepultus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mendozasaurus neguyelap	?	?	?	?	?	0	?	0	1	?	?	?	?	?	?	?	?	0	0	1	?	?	?	?	?	?	?	?	?	?
Malawisaurus dixeyi	?	1	2	0	0	0	?	0	1&2	0	1	?	1	0	1	1	1	0	?	1	1	1	1	0	?	?	?	0	2	1
Argentinosaurus hunculensis	1	0	0	?	0	0	0	0	1	?	1	1	1	?	1	1	1	1	0	1	1	1	1	0	0	?	0	0	2	1
Dreadnoughtus schrani	1	1	2	0	0	0	0	0	1	0	1	1	0&1	?	1	1	1	1	0	1	1	1	1	0	0	1	?	0	2	1
Epachthosaurus sciuttoi	?	0	0	?	0	0	0	0	2	?	1	1	1	?	2	1	1	1	0	1	1	1	1	0	0	1	0	0	2	1
Rapetosaurus krausei	1	1	2	0	0	0	1	0	2	0	1	1	0	-	1	0	1	1	0	1	1	1	1	0	0	1	0	1	2	1
Muyelensaurus pecheni	?	1	2	0	0	0	1	0	1	0	1	1	0	-	1	0	1	1	0	1	1	0	-	0	0	1	?	0	2	1

Table S.51. Data matrix

Taxa	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210
Rinconsaurus caudamirus	?	1	2	0	?	0	1	0	2	?	?	1	0	-	1	?	1	?	0	?	1	0	-	?	0	1	?	?	2	1
Overosaurus paradasorum	1	1	2	0	?	0	?	0	2	?	1	0	0	-	?	?	1	1	0	?	1	1	1	?	?	?	?	1	2	1
Aelosaurus rionegrinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus maximus	?	1	2	0	?	?	1	?	?	0	?	?	?	?	?	0	1	?	?	?	1	?	?	?	0	1	?	?	2	1
Aelosaurus colhuehuapensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapuiasaurus macedoi	?	1	2	0	0	0	?	0	1	0	1	1	0	-	?	0	1	1	0	?	1	1	?	0	0	?	?	?	?	1
Gondwanatitan faustoi	?	1	2	0	?	?	?	0	2	?	?	?	0	-	?	0	?	?	?	?	?	?	?	?	?	?	?	?	2	1
Ampelosaurus atacis	?	0	?	?	-	?	?	0	2	0	1	?	1	?	0	1	1	?	0	?	1	0	-	0	1	2	?	?	?	?
EC1	1	0	?	?	-	?	0	0	2	0	1	?	?	?	0	1	1	1	0	?	1	?	?	?	1	2	0	?	2	?
Lirainosaurus astibiae	1	1	2	0	0	0	0	0	1	0	1	1	?	?	0	1	1	0	0	?	1	0	-	0	1	2	0	0	2	1
Diamantinasaurus matildae	2	?	?	?	?	0	0	0	0	0	1	1	1	?	0	2	1	?	0	?	1	0	-	0	?	?	?	?	2	?
Isisaurus colberti	?	1	2	0	0	0	1	0	0	0	1	1	1	0	0	0	1	0	0	1	1	0	-	0	0	0	0	1	2	1
Opisthocoelicaudia skarzynskii	2	1	2	0	0	0	1	0	2	0	1	1	1	0	2	1	1	1	0	1	1	1	1	0	0	?	?	1	2	1
Alamosaurus sanjuanensis	2	1	2	0	0	0	0	0	2	0	1	1	0	-	2	1	1	?	0	1	1	1	1	0	0	1	?	0	2	1
Saltasaurus loricatus	1	1	2	0	0	0	0	0	2	0	1	1	1	0	1	1	1	1	0	1	1	0	-	0	0	0	0	1	2	1
Neuquensaurus australis	1	1	2	0	0	0	0	0	2	?	1	1	1	0	2	1	1	1	0	1	1	0	-	0	0	0	0	1	2	1
Baurutitan britoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trigonosaurus pricei	0&2	1	2	0	0	0	1	0	2	?	1	1	1	?	2	1	1	1	0	1	1	0	-	0	0	0	0	1	2	1

Table S.51. Data matrix

Taxa	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230	231	232	233	234	235	236	237	238	239	240
Plateosaurus	0	?	0	?	?	?	?	?	?	?	?	?	?	?	0	?	0	0	0	?	?	0	0	?	?	0	?	?	?	0
Antetonitrus ingenipes	0	?	?	?	?	1	?	?	?	?	0	?	?	?	?	?	0	?	?	?	?	0	?	?	?	0	?	?	?	0
Vulcanodon karibaensis	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	0	?	0	?	?	?	?	?	0
Tazoudasaurus naimi	0	?	0	0	0	0	0	0	0	?	0	0	?	?	?	?	?	?	?	?	?	0	?	0	0	0	0	?	0	0
Barapasaurus tagorei	0	?	?	?	0	0	0	?	?	?	0	?	0	1	1	0	0	?	?	?	?	0	?	0	?	0	?	?	?	0
Shunosaurus lii	0	0	0	1	0	1	?	0	0	0	0	0	0	1	0	?	0	0	0	0	1	0	1	0	0	0	0	?	0	0
Patagosaurus fariasi	0	0	0	0	0	0	0	0	0	?	0	0	0	2	?	?	0	?	?	?	?	?	?	?	?	0	?	?	?	0
Cetiosaurus oxoniensis	0	?	?	0	0	0	0	?	0	?	?	0	?	?	?	?	?	?	1	0	?	0	?	0	0	0	0	?	0	0
Cetiosauriscus stewerti	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	0	?	?	?	0	0	?	0	2
Omeisaurus	0	0	0	0	?	0	0	0	0	0	0	0	?	2	1	1	0	1	1	0	0	0	1	0	0	0	0	?	0	0
Mamenchisaurus	0	?	0	?	1	0	0	0	0	0	0	0	0	2	?	?	0	?	?	0	0	0	1	1	0	0	0	0	0	3
Chuanjiesaurus anaensis	?	?	?	?	?	0	0	?	?	?	0	?	?	1	?	?	?	?	?	?	?	?	1	1	0	0	0	?	0	3
Bellusaurus sui	0	?	?	?	0	?	?	0	0	?	?	?	?	2	?	?	0	?	?	?	?	0	?	1	0	0	?	0	?	3
Lapparentosaurus madagascariensis	0	0	0	0	0	1	0	?	0	?	0	0	0	?	?	?	?	1	0	0	?	0	?	?	?	?	?	?	0	0
Jobaria tiguidensis	0	?	0	?	0	1	?	?	0	?	0	0	0	2	1	1	0	1	1	?	1	0	1	0	0	0	0	?	0	0
Losillasaurus giganteus	0	0	?	0	?	0	0	?	0	?	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0	0	0	0	2
Turiasaurus riodevensis	0	0	0	?	1	0	0	0	0	?	?	0	0	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Zby atlanticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Haplocanthosaurus priscus	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1	0	1	1	?	?	0	1	0	0	0	0	0	0	0
Amazonsaurus maranhensis	?	?	0	0	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?	?	?	0
Zapalasaurus bonapartei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	0
Rayosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Histriasaurus boscarollii	0	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rebbachisaurus	0	0	?	1	?	1	2	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Limaysaurus tessonei	0	?	0	1	0	1	1	?	?	?	?	0	?	?	?	?	?	?	?	?	1&2	0	1	0&2	0	1	?	?	?	4
Cathartesaura anaerobica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	0	?
Comahuesaurus windhauseni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	2	0	1	0	?	0	4
Demandasaurus darwini	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	1	0	1	0	4
Nigersaurus taqueti	0	?	0	1	?	?	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	4
Dicraeosaurus	0	0	1	0	1	1	2	0	?	0	1	0	0	2	1	?	1	?	?	0	?	0	?	1	0	0	0	0	0	2
Amargasaurus cazaui	0	?	1	0	1	1	2	?	?	?	0	?	0	2	?	?	1	?	?	0	?	?	?	0	?	0	?	?	?	?
Brachytrachelopan mesai	0	?	1	?	?	1	2	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Suuwassea emilieae	?	?	?	?	1	?	1	?	?	?	?	0	0	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	1
Apatosaurus	0	0	0	0	1	1	1	0	0	0	0&1	1	0	2	1	?	1	1	1	?	2	0	1	1	0	0	0	0	0	2
Tornieria africana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0	?	?	0	2
Supersaurus vivianae	?	?	1	0	?	1	1	?	0	?	0	?	?	2	?	?	?	1	?	?	?	?	?	?	?	0	?	?	0	2
Barosaurus lentus	0	0	1	0	1	1	1	0	0	0	0	0	0	2	1	1	1	1	1	?	?	0	1	1	0	0	?	?	0	2
Kateedocus siberi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230	231	232	233	234	235	236	237	238	239	240
Diplodocus	0	0	1	0	1	1	1	0	0	0	1	0	0	2	1	1	1	1	1	0	2	0	1	?	0	0	0	0	0	2
SHN (JJS) 177	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	?	0	?	1	?	0	0	?	?	2
Dinheirosaurus lourinhanensis	0	0	?	?	?	1	1	0	0	0	?	1	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	2
Camarasaurus	0	0	0	0	1	0	0	0	0	0	0	0	?	2	1	1	0	1	1	0	1	0	1	0	0	0	0	0	0	0&1
Lourinhasaurus alenquerensis	?	?	0	?	1	?	?	?	?	?	?	0	1	2	?	?	?	1	1	0	?	0	?	?	?	0	0	0	0	1
SHN 181	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	0	?	?	?	0	0	?	?	1
Tehuelchesaurus benetezii	1	0	0	?	0	0	?	?	1	?	?	0	1	?	1	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?
Aragosaurus ischiaticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0	0	0	0	1
Galveosaurus herreroi	?	?	?	?	0	0	0	?	0	?	?	0	?	2	1	1	0	?	?	0	?	0	?	?	?	0	?	?	?	1
Europasaurus holgeri	0	0	0	0	0	0	0	0	0	?	0	0	0	2	1	?	0	0	1	0	?	0	1	0	0	0	0	0	0	0
Lusotitan atalaiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	0	?	?	?	0	?	0	0	1
Brachiosaurus altithorax	1	0	0	?	0	0	0	?	1	1	0	1	1	2	1	?	0	?	1	?	0	?	?	?	?	0	1	?	1	1
Giraffatitan brancai	0&1	0	0	0	0	0	0	1	1	1	0	1	1	2	1	1	0	1	1	?	?	0	1	0	0	0	1	0	1	1
Abydosaurus mcintoshi	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	1	?	1	?
Venenosaurus dicrocei	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	0	?	2	?	0	1	?	1	1
Sonorasaurus thompsoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Cedarosaurus weiskopfae	1	0	0	?	?	?	0	?	?	?	?	?	1	?	?	?	?	?	?	?	?	0	?	?	?	0	?	?	?	1
Sauroposeidon proteles	1	0	0	?	?	0	0	0	1	?	0	1	1	2	1	?	?	?	1	?	?	0	?	?	?	1	0	?	?	1
Tastavinsaurus sanzi	1	0	?	?	0	0	0	?	1	?	0	1	1	2	1	1	0	1	1	0	0	0	1	2	0	0	1	0	1	1
Huabeisaurus allocotus	0	0	?	0	?	0	0	?	0	?	?	1	1	3	1	?	0	1	?	?	?	0	2	?	?	0&1	0	0	0	1
Phuwiangosaurus sirindhornae	0	0	0	0	0	0	0	1	0	?	0	1	1	?	?	?	0	1	1	?	?	0	?	0	0	0	0	0	0	1
Tangvayosaurus hoffeti	1	0	?	?	?	?	?	?	0	?	?	1	1	?	?	?	?	?	?	?	?	0	1	0	0	?	?	?	?	1
Yunmenglong ruyangensis	1	0	?	0	?	0	0	?	0	?	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	1
Qiaowanlong kangxii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euhelopus zdanskyi	1	0	0	0	1	0	?	0	0	0	0	1	1	3	?	?	0	1	1	?	?	?	?	?	?	?	?	?	?	?
Erketu ellisoni	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Daxiatitan binglingi	0	?	?	?	?	0	?	1	1	0	?	1	1	?	?	?	?	?	?	?	?	1	?	?	?	0	?	?	?	3
Chubutisaurus insignis	0	0	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	0	1	0	?	0	0	?	0	1
Ligabuesaurus leanzai	1	?	0	?	0	1	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Wintonotitan wattsi	?	?	?	?	?	?	?	1	?	?	?	1	1	?	?	?	?	?	0	1	?	0	?	?	?	0	0	?	?	1
Andesaurus delgadoi	1	0	?	?	0	?	?	?	1	?	?	?	1	?	?	?	?	?	0	?	0	0	1	?	1	0	1	?	?	2
Rukwatitan bisepultus	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	3
Mendozasaurus neguyelap	?	?	?	?	0	?	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0	0	1	1	3
Malawisaurus dixeyi	1	0	0	?	0	0	0	1	1	?	0	1	1	?	?	?	?	?	?	?	?	1	1	?	?	0	0	1	1	3
Argentinosaurus huncullensis	1	?	?	?	?	?	?	1	1	?	0	1	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?
Dreadnoughtus schrani	1	0	0	0	0	0	0	1	1	0	0	?	1	?	?	?	?	?	?	?	?	0	1	3	?	0	0	?	0	3
Epachthosaurus sciuttoi	1	0	0	?	0	0	0	?	1	?	0	1	0	3	?	?	?	?	1	?	?	?	2	1	0	0	0	?	0	3
Rapetosaurus krausei	1	0	0	0	0	0	0	1	1	1	0	1	?	3	?	?	?	?	1	1	?	0	1	?	?	0	?	0	?	3
Muyelensaurus pecheni	?	?	0	0	0	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	3

Table S.51. Data matrix

Taxa	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230	231	232	233	234	235	236	237	238	239	240
Rinconsaurus caudamirus	1	?	?	?	?	0	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	3
Overosaurus paradasorum	1	1	0	0	0	0	0	1	1	0	0	1	?	3	1	1	0	1	?	?	?	1	1	1	?	?	?	?	0	3
Aelosaurus rionegrinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	3
Aelosaurus maximus	?	?	?	0	0	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	0	?	?	?	0	?	?	?	3
Aelosaurus colhuehuapensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	?	?	?	?	?	3
Tapuiasaurus macedoi	?	1	?	?	0	1	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gondwanatitan faustoi	1	?	?	?	?	?	?	?	?	?	?	1	?	3	1	?	?	?	0	1	?	0	?	?	?	?	?	?	?	3
Ampelosaurus atacis	?	1	0	?	0	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	0	0	0	3
EC1	1	1	0	0	0	?	0	?	?	?	?	1	1	3	1	1	0	1	?	1	?	0	2	1	0	0	0	0	0	3
Lirainosaurus astibiae	0	1	?	0	?	0	0	?	1	?	0	1	?	?	?	?	?	?	?	?	?	0	?	?	?	0	?	0	1	3
Diamantinasaurus matildae	0	?	?	?	?	0	0	?	1	?	?	1	1	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?
Isisaurus colberti	0	?	0	0	0	1	1	0	1	0	0	?	1	3	1	1	0	?	0	?	?	?	?	?	?	0	0	0	?	3
Opisthocoelicaudia skarzynskii	0	1	?	0	1	0	0	1	1	1	?	1	1	3	1	?	0	?	0	?	0	?	2	2	1	0	?	?	?	-
Alamosaurus sanjuanensis	0	1	0	0	0	0	0	0	1	0	0	1	1	?	1	?	0	?	?	1	0	1	2	3	1	0	0	?	0	3
Saltasaurus loricatus	1	1	0	0	0	0	0	1	1	?	0	?	?	3	1	1	0	1	0	1	?	1	?	1	?	0	0	0	0	3
Neuquensaurus australis	1	1	0	0	0	0&1	0	1	1	?	0	?	?	3	1	?	0	1	?	?	?	1	?	3	0	0	0	0	0	3
Baurutitan britoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	3	1	0	0	0	0	3
Trigonosaurus pricei	1	1	0	?	0	0	0	1	1	0	0	?	?	3	1	1	0	1	?	?	?	?	1	?	?	0	0	0	0	3

Table S.51. Data matrix

Taxa	241	242	243	244	245	246	247	248	249	250	251	252	253	254	255	256	257	258	259	260	261	262	263	264	265	266	267	268	269	270
Plateosaurus	-	0	0	?	?	?	0	?	0	?	?	?	0	?	0	0	0	-	?	?	0	0	0	?	?	?	?	?	?	0
Antetonitrus ingenipes	-	?	0	?	?	?	0	?	0	?	?	?	0	?	?	?	0	-	?	?	0	0	?	?	?	?	?	?	?	?
Vulcanodon karibaensis	-	0	0	?	?	?	1	?	?	?	0	?	?	?	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	0
Tazoudasaurus naimi	-	?	0	0	0	0	0	?	0	?	0	?	0	0	?	1	0	0	1	?	0	0	0	0	?	?	?	?	?	?
Barapasaurus tagorei	-	0	0	?	0	0	0	?	0	?	0	?	0	?	0	1	0	0	?	?	0	?	?	?	?	?	?	?	?	0
Shunosaurus lii	-	0	0	0	0	0	?	?	0	?	0	0	0	0	0	1	0	0	1	0	0	0	0	?	?	0	0	1	0	0
Patagosaurus fariasi	-	0	0	?	0	0	?	?	0	?	?	?	?	0	0	1	?	?	1	?	?	?	?	?	?	?	?	?	?	0
Cetiosaurus oxoniensis	-	0	0	0	0	0	0	0	0	0	0	?	0	0	?	?	0	-	1	0	0	?	0	0	?	?	?	?	?	0
Cetiosauriscus stewerti	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	-	1	0	0	0	1	0	0	0	0	1	0	0
Omeisaurus	-	0	0	0	0	0	?	0	0	?	0	1	0	0	0	1	0	0	1	0	0	0	0	?	0	0	0	0	?	0
Mamenchisaurus	0	0	0	0	0	0	?	0	0	?	0	?	0	0	0	1	0	0	1	0	0	0	0	?	?	0	0	0	0	0
Chuanjiesaurus anaensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?	0	0	0	?	?	?	0	0	0	?	0
Bellusaurus sui	?	?	0	?	0	0	0	?	0	?	0	?	1	?	?	1	0	?	1	0	0	0	1	?	?	0	0	0	?	?
Lapparentosaurus madagascariensis	-	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	-	1	?	0	0	1	?	?	0	0	?	0	?
Jobaria tiguidensis	-	0	0	?	?	?	0	0	0	?	0	1	0	?	0	1	0	0	?	0	0	0	1	?	0	0	0	?	0	0
Losillasaurus giganteus	0	0	0	0	0	0	0	?	1	0	0	1	0	0	0	1	0	0	1	?	0	0	1	0	0	0	0	0	0	0
Turiasaurus riodevensis	?	?	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Zby atlanticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Haplocanthosaurus priscus	-	0	0	0	0	0	0	0	0	?	0	?	0	0	0	1	1	0	1	0	0	?	1	0	0	0	0	0	0	0
Amazonsaurus maranhensis	-	?	0	?	0&1	0&1	0	?	0	?	?	?	1	1	?	?	?	?	0	?	1	0&1	1	1	0	0	0	?	0	?
Zapalasaurus bonapartei	-	?	0	?	1	1	0	?	0	?	0	?	1	?	?	1	0	?	0	1	1	0	0	?	?	0	0	?	0	?
Rayosaurus	?	0	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Histriasaurus boscarollii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rebbachisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Limaysaurus tessonei	-	?	0	?	0	0	0	?	0	?	0	?	1	?	?	1	0	0	0	0	1	1	?	?	0	0	0	1	0	?
Cathartesaura anaerobica	?	?	?	?	?	?	0	0	0	?	1	?	1	?	?	?	0	0	0	?	1	1	?	1	0	0	0	1	0	?
Comahuesaurus windhauseni	-	?	0	?	0	0	0	?	0	?	0	?	?	?	?	1	0	?	0	?	?	?	?	?	?	?	?	?	?	?
Demandasaurus darwini	-	?	0	0	0	0	1	0	1	?	0	?	1	1	0	1	0	0	1	?	1	0	1	?	1	0	0	1	0	0
Nigersaurus taqueti	-	?	0	?	?	?	?	?	1	?	?	?	1	?	?	?	0	?	0	?	1	0	1	1	1	0	0	1	0	?
Dicraeosaurus	?	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	1	0	1	1	0	0	0	?	?	0
Amargasaurus cazaui	?	?	0	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	1	0	?	?	0	?	?	?	?	0
Brachytrachelopan mesai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Suuwassea emilieae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apatosaurus	0	0	0	1	0	0	0	0&1	0	?	1	?	1	1	0	1	1	1	1	0	1	1	1	1	0	0	0	1	0	0
Tornieria africana	?	0	1	-	1	1	1	0	0	0	1	0	1	1	?	1	1	?	?	1	1	1	1	1	0	1	0	?	0	0
Supersaurus vivianae	?	0	1	-	1	1	1	0	1	?	1	?	1	?	?	?	1	?	?	0	1	1	1	0	0	1	0	0	0	?
Barosaurus lentus	?	0	1	-	1	1	1	0	0	?	1	0	1	1	0	1	1	1	1	1	1	?	1	1	0	1	1	1	1	0
Kateedocus siberi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	241	242	243	244	245	246	247	248	249	250	251	252	253	254	255	256	257	258	259	260	261	262	263	264	265	266	267	268	269	270
Diplodocus	0	0	1	-	1	1	1	1	0	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0
SHN (JJS) 177	0	0	1	-	1	1	1	1	0	1	1	0	1	1	0	1	1	?	1	?	1	1	1	1	0	1	1	1	1	0
Dinheirosaurus lourinhanensis	0	0	1	-	1	1	1	?	?	?	?	?	1	1	?	?	?	?	?	?	1	?	?	1	?	1	1	?	1	?
Camarasaurus	-	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Lourinhasaurus alenquerensis	-	0	0	0	0	0	0	0	0	0	0	?	1	0	0	1	0	0	1	?	0	0	1	0	0	0	0	0	0	?
SHN 181	-	0	0	0	0	0	0	0	0	0	0	?	1	0	?	1	0	0	?	?	0	0	1	0	0	0	0	0	?	0
Tehuelchesaurus benetezii	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aragosaurus ischiaticus	-	0	0	0	0	0	0	0	0	0	0	?	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Galveosaurus herreroi	-	0	0	0	0	0	0	?	?	0	?	1	?	?	?	1	0	0	?	0	?	?	?	?	?	?	?	?	?	?
Europasaurus holgeri	-	0	0	0	0	0	0	?	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Lusotitan atalaiensis	-	0	0	1	0	0	0	0	?	0	0	1	?	?	0	1	0	0	1	0	0	?	1	?	0	?	?	?	0	0
Brachiosaurus altithorax	-	0	?	?	?	?	0	0	0	?	0	?	?	0	0	1	?	?	1	?	?	?	?	0	?	0	0	0	?	?
Giraffatitan brancai	-	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	?	1	0	0	0	0	0	0	0
Abydosaurus mcintoshi	?	?	?	1	?	?	0	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Venenosaurus dicrocei	-	0	0	1	0	?	0	?	0	?	0	1	0	?	0	1	0	0	1	0	0	0	1	?	0	0	0	0	?	?
Sonorasaurus thompsoni	-	?	?	0	?	?	0	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cedarosaurus weiskopfae	-	0	0	1	?	?	0	?	0	0	0	1	0	0	?	1	0	?	0	?	0	0	1	0	?	0	0	0	?	0
Sauroposeidon proteles	-	0	0	0	?	?	0	?	0	?	0	1	1	0	0	1	0	0	0	0	0	0	1	0	?	0	0	0	?	0
Tastavinsaurus sanzi	-	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Huabeisaurus allocotus	-	0	0	0	0	1	0	0	?	0	0	1	1	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	?	?
Phuwiangosaurus sirindhornae	-	0	0	0	?	1	0	0	0	?	0	1	0	0	0	1	0	0	1	0	0	0	1	1	?	0	0	0	?	0
Tangvayosaurus hoffeti	-	?	0	0	?	?	0	?	?	?	0	1	0	?	?	1	0	0	?	0	?	0	?	?	?	?	?	?	?	?
Yunmenglong ruyangensis	-	0	0	?	?	?	?	?	0	?	0	1	1	?	0	1	0	0	1	?	?	?	1	?	0	0	0	0	?	?
Qiaowanlong kangxii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euhelopus zdanskyi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
Erketu ellisoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Daxiatitan binglingi	0	0	?	0	?	?	?	?	?	?	0	0	?	?	0	1	0	-	?	?	?	?	?	?	?	?	?	?	?	0
Chubutisaurus insignis	-	?	0	0	0	0	0	?	?	0	0	1	?	?	?	1	0	-	?	0	?	-	?	?	?	?	?	?	?	?
Ligabuesaurus leanzai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Wintonotitan wattsi	-	0	0	0	0	0	0	?	?	0	0	1	?	?	?	1	?	?	0	0	?	?	?	?	?	?	?	?	0	?
Andesaurus delgadoi	0	0	0	0	1	1	0	?	0	0	0	1	0	?	?	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?
Rukwatitan bisepultus	1	0	0	0	0	0	0	?	0	0	0	1	?	2	0	1	?	?	0	0	0	0	1	1	?	0	0	0	0	0
Mendozasaurus neguyelap	1	0	0	?	0	0	?	0	0	?	0	?	0	2	0	1	0	0	0	0	0	0	1	1	?	?	?	?	?	0
Malawisaurus dixeyi	1	0	0	1	0	?	1	0	0	0	0	1	0	2	0	1	0	0	?	?	0	0	1	1	?	0	0	0	?	0
Argentinosaurus hunculensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dreadnoughtus schrani	1	0	0	0	0	0	0	0	0	0	0	1	0	2	0	1	0	0	0	0	0	0	1	1	?	0	0	0	0	0
Epachthosaurus sciuttoi	1	0	0	?	?	?	1	?	0	0	0	1	0	2	0	1	0	0	1	0	0	0	1	1	?	0	0	0	0	0
Rapetosaurus krausei	1	1	?	0	?	?	?	0	?	?	?	?	?	2	0	1	0	0	0	?	0	?	?	1	?	?	?	?	?	0
Muyelensaurus pecheni	0	1	0	?	?	?	?	0	0	?	0	?	0	2	0	1	0	0	?	?	0	-	1	?	0	0	0	0	?	0

Table S.51. Data matrix

Taxa	241	242	243	244	245	246	247	248	249	250	251	252	253	254	255	256	257	258	259	260	261	262	263	264	265	266	267	268	269	270
Rinconsaurus caudamirus	0	0	0	1	0	0	0	?	?	0	0	?	0	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Overosaurus paradasorum	1	1	0	0	0	0&1	1	?	?	0	0	?	?	?	0	1	0	0	?	0	?	?	?	?	?	?	?	?	?	1
Aelosaurus rionegrinus	1	1	0	1	?	?	1	?	?	0	0	?	?	?	1	1	0	0	?	?	0	0	?	?	?	?	?	?	?	1
Aelosaurus maximus	0	1	0	0	1	0	1	?	0	0	0	1	0	2	1	1	0	0	0	?	0	0	?	?	?	?	?	?	0	0
Aelosaurus colhuehuapensis	0	1	0	1	?	?	1	?	?	0	0	?	?	?	1	1	0	0	?	0	0	0	1	?	?	?	?	?	?	1
Tapuiasaurus macedoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gondwanatitan faustoi	0	1	0	1	1	?	1	?	?	0	0	1	0	?	0	1	0	0	?	0	0	0	?	?	?	?	?	?	?	1
Ampelosaurus atacis	?	0	0	0	?	?	0	0	0	0	0	?	?	?	0	?	0	?	?	?	0	0	?	1	?	0	0	0	?	1
EC1	1	0	0	0	1	0	0	0	0	0	0	1	1	?	0	1	0	0	0	0	0	0	1	1	?	0	0	0	0	1
Lirainosaurus astibiae	1	0	0	0	0	?	0	0	0	0	0	?	0	2	0	1	0	0	0	?	0	0	1	?	?	?	?	0	0	1
Diamantinasaurus matildae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Isisaurus colberti	0	0	0	?	?	1	1	0	0	0	0	?	1	2	0	1	0	0	1	0	0	0	1	1	?	0	0	0	0	0
Opisthocoelicaudia skarzynskii	-	0	0	0	1	1	1	0	0	0	0	?	1	2	0	?	0	0	1	0	0	0	1	1	?	0	0	0	?	0
Alamosaurus sanjuanensis	0	0	0	?	0	1	1	0	0	?	0	1	1	?	0	1	0	0	0	0	0	0	1	?	?	0	0	0	?	0
Saltasaurus loricatus	0	0	0	0	1	1	1	0	0	1	0	1	1	0	0	1	0	0	?	?	0	0	1	1	?	0	0	0	?	0
Neuquensaurus australis	0	0	0	?	?	?	1	0	0	1	0	?	1	0	0	1	0	0	?	?	0	0	1	?	?	?	?	?	?	0
Baurutitan britoi	0	0	0	0	1	0	0	0	0	0	0	1	1	2	0	1	0	0	0	0	0	0	1	1	?	0	0	0	0	0
Trigonosaurus pricei	0	0	0	0	?	?	?	0	0	?	0	1	?	2	0	1	0	0	0	0	0	0	1	1	?	0	0	0	0	?

Table S.51. Data matrix

Taxa	271	272	273	274	275	276	277	278	279	280	281	282	283	284	285	286	287	288	289	290	291	292	293	294	295	296	297	298	299	300
Plateosaurus	0	0	0	2	0	0	0	1	0	0	0	0	?	0	?	?	?	?	?	?	?	0	?	?	?	?	0	?	0	0
Antetonitrus ingenipes	0	0	0	2	?	?	0	?	0	0	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	0	0
Vulcanodon karibaensis	0	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	0	?	0	?
Tazoudasaurus naimi	0	0	0	2	?	?	0	2	0	0	0	0	?	?	0	0	0	0	?	1	0	0	0	?	?	?	?	?	0	0
Barapasaurus tagorei	0	0	?	1	0	0	?	?	?	0	?	0	?	0	0	?	?	?	?	1	?	0	0	?	0	?	0	?	0	0
Shunosaurus lii	0	0	0	2	0	0	0	1	?	0	0	?	?	?	0	?	?	?	?	1	0	1	0	1	0	0	0	0	0	0
Patagosaurus fariasi	0	0	0	2	0	?	0	2	?	0	?	?	?	?	0	?	?	?	?	?	?	0	0	?	?	?	0	?	1	0
Cetiosaurus oxoniensis	0	0	1	2	?	?	0	?	0	0	0	?	?	?	0	?	1	0	0	?	?	?	?	?	?	?	?	?	0	0
Cetiosauriscus stewerti	0	0	0	2	0	0	0	2	0	0	0	?	?	?	0	0	0	0	?	1	?	0	0	?	1	0	0	?	?	0
Omeisaurus	0	0	0	2	0	0	0	1	0	0	0	?	?	?	0	0	?	?	?	1	0	0	0	0	0	0	0	0	1	0
Mamenchisaurus	0	0	0	2	0	0	0	2	0	0	?	?	?	?	?	0	0	?	?	1	1	0	0	?	0	?	0	0	1	0
Chuanjiesaurus anaensis	?	0	0	2	0	0	0	2	0	?	0	?	?	?	0	0	0	0	0	1	1	0	0	?	?	?	?	?	1	0
Bellusaurus sui	0	0	0	?	?	?	0	?	0	0	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	1	0
Lapparentosaurus madagascariensis	0	0	0	?	?	?	0	?	0	0	0	?	?	?	0	0	0/1	0	?	?	?	?	?	?	?	?	?	?	1	0
Jobaria tiguidensis	0	0	0	2	0	0	0	1	?	0	?	?	?	?	?	?	?	?	?	1	?	0	0	1	0	0	0	?	1	0
Losillasaurus giganteus	0	?	?	?	?	?	?	1	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Turiasaurus riodevensis	?	?	?	?	?	?	?	?	2	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Zby atlanticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	0
Haplocanthosaurus priscus	0	0	0	2	0	?	0	1	0	?	?	?	?	?	0	0	0	0	0	?	?	1	0	?	?	?	0	?	1	0
Amazonsaurus maranhensis	1	0	0	2	?	?	1	?	0	0	?	?	?	?	?	0	?	0	0	?	?	1	0	?	?	?	?	?	?	?
Zapalasaurus bonapartei	1	0	0	2	?	?	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rayosaurus	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	1
Histriasaurus boscarollii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rebbachisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1
Limaysaurus tessonei	1	0	0	2	?	?	1	1	0	0	1	1	?	1	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	1
Cathartesaura anaerobica	1	0	0	2	?	?	1	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1
Comahuesaurus windhauseni	1	0	0	2	0	0	1	1	?	0	?	?	?	?	0	1	0	0	?	?	?	1	0	?	?	?	?	?	?	?
Demandasaurus darwini	0	0	0	2	?	?	?	?	0	0	?	?	?	?	?	0	0	1	?	?	?	1	0	?	?	?	?	?	?	?
Nigersaurus taqueti	1	0	0	2	?	0	1	1	0	0	1	1	?	1	?	?	0	?	?	1	1	?	0	?	?	?	?	?	1	1
Dicraeosaurus	0	0	0	2	0	0	1	2	?	0	?	1	?	1	0	0	0	0	0	1	?	0	0	?	?	?	0	?	1	0
Amargasaurus cazaui	?	0	?	2	0	0	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?
Brachytrachelopan mesai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Suuwassea emilieae	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0
Apatosaurus	0	0	0	2	0	0	1	2	?	?	1	1	1	1	0	0	0	0	0	1	0	0	0	1	0	?	0	0	1	0
Tornieria africana	2	0	0	3	?	0	1	?	?	?	?	?	?	?	0	1	0	0	0	?	?	?	?	?	?	?	?	?	1	0
Supersaurus vivianae	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	0	?	?	?	?	?	0	?	?	?	?	?	?	1	0
Barosaurus lentus	2	0	0	3	0	0	1	2	?	0	1	1	?	1	1	1	?	?	0	1	?	0	0	?	0	?	0	?	1	0
Kateedocus siberi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	271	272	273	274	275	276	277	278	279	280	281	282	283	284	285	286	287	288	289	290	291	292	293	294	295	296	297	298	299	300
Diplodocus	2	0	0	3	0	0	1	2	?	0	1	1	1	1	1	0&1	0	0	0	1	1	0	0	1	0	?	0	?	1	0
SHN (JJS) 177	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	0	0	?	?	?	?	?	?	?
Dinheirosaurus lourinhanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Camarasaurus	0	0	0	2	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0&1	1	0&1	0	1	0	0	0	0	1	0
Lourinhasaurus alenquerensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	1	0
SHN 181	0	?	?	?	0	?	0	?	?	?	?	?	?	?	0	?	0	?	?	?	?	1	0	?	?	1	?	?	1	?
Tehuelchesaurus benetezii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0
Aragosaurus ischiaticus	0	0	0	2	0	0	0	1	0	0	0	?	?	?	0	0	?	0	0	0	-	1	0	?	0	1	0	?	1	0
Galveosaurus herreroi	0	0	1	?	?	?	0	?	0	0	0	?	?	?	0	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?
Europasaurus holgeri	0	0	1	2	0	0	0	1	0	0	0	0	?	0	0	1	0	0	?	?	?	1	1	?	?	?	?	?	1	0
Lusotitan atalaiensis	0	0	1	?	0	?	0	?	?	?	?	?	?	?	0	0	1	1	0	0	-	0	1	?	0	1	0	?	?	?
Brachiosaurus altithorax	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Giraffatitan brancai	0	0	1	2	0	0	0	1	0	0	0	1	?	0	0	0	1	1	0	0	-	1	1	?	?	1	0	1	1	0
Abydosaurus mcintoshi	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
Venenosaurus dicrocei	0	0	1	0	?	?	0	?	0	0	0	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	1	0
Sonorasaurus thompsoni	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cedarosaurus weiskopfae	0	1	1	0	0	?	0	0	1	0	0	?	?	?	0	?	1	?	0	?	?	1	1	?	?	0	?	?	?	0
Sauroposeidon proteles	0	0	1	2	0	0	0	1	0	0	0	0	?	?	?	?	1	0	?	0	-	1	?	?	?	?	?	?	1	0
Tastavinsaurus sanzi	0	0	1	0	0	0	0	0	1	0	0	?	?	?	0	1	1	1	0	0	-	1	?	1	1	1	0	1	?	?
Huabeisaurus allocotus	1	0	1	2	0	0	0	1	0	0	0	?	?	?	0	0	0	0	0	0	-	1	1	?	1	1	0	?	1	?
Phuwiangosaurus sirindhornae	1	0	1	1	?	?	0	1	0	0	0	0&1	0	0	0	0	?	?	?	0	-	1	0	1	?	1	?	?	1	0
Tangvayosaurus hoffeti	0	0	1	2	?	0	?	?	?	0	?	1	0	0	?	?	?	?	?	0	-	1	1	1	?	1	?	?	?	?
Yunmenglong ruyangensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	0	-	?	?	?	?	?	?	?	?	?
Qiaowanlong kangxii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euhelopus zdanskyi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0
Erketu ellisoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Daxiatitan binglingi	?	0	1	?	0	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	1	0
Chubutisaurus insignis	0	0	1	?	?	?	0	?	0	0	0	?	?	?	?	?	1	0	?	?	?	1	?	?	?	?	?	?	1	0
Ligabuesaurus leanzai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0
Wintonotitan wattsi	0	0	1	?	?	?	0	?	0	0	0	1	?	0	0	?	1	0	?	?	?	1	0	?	?	0	?	?	1	0
Andesaurus delgadoi	0	0	1	2	0	0	0	1	0	?	0	?	?	?	0	?	?	?	0	?	?	1	?	?	?	0	?	1	?	?
Rukwatitan bisepultus	0	0	1	2	0	0	0	?	?	?	?	?	?	?	0	0	0	0	0	?	?	1	?	?	?	?	?	?	?	?
Mendozasaurus neguyelap	0	2	1	2	0	1	0	1	0	0	?	?	?	?	?	0	?	0	0	?	?	1	1	?	?	1	1	?	1	0
Malawisaurus dixeyi	0	2	1	2	0	1	0	1	0	0	?	?	?	?	0	0	0	0	0	0	-	1	1	?	?	0	0	1	?	?
Argentinosaurus hunculensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dreadnoughtus schrani	0	3	1	0&1	0	1	0	0	1	0	0	?	?	?	0	?	?	?	0	0	-	1	1	1	0	?	?	1	1	0
Epachthosaurus sciuttoi	0	3	1	1	0	1	?	0	1	0	0	?	?	?	0	1	1	?	0	?	?	?	?	?	?	?	?	?	?	?
Rapetosaurus krausei	?	3	?	2	?	2	0	1	1	?	0	?	?	?	?	?	0	0	?	?	?	1	1	1	0	?	?	?	1	0
Muyelensaurus pecheni	?	3	1	2	0	1	0	1	1	?	0	?	?	?	0	?	0	?	1	?	?	?	?	?	?	?	?	?	1	0

Table S.51. Data matrix

Taxa	271	272	273	274	275	276	277	278	279	280	281	282	283	284	285	286	287	288	289	290	291	292	293	294	295	296	297	298	299	300
Rinconsaurus caudamirus	0	3	1	2	0	1	0	?	1	1	0	1	?	0	0	?	0	0	1	0	-	1	?	?	?	?	0	?	?	?
Overosaurus paradasorum	?	3	1	?	1	1	?	?	?	?	?	?	?	?	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus rionegrinus	0	?	?	0	1	2	?	?	?	?	?	?	?	?	?	?	?	?	0	0	-	1	0	?	?	1	1	?	1	?
Aelosaurus maximus	0	3	1	0	1	2	?	?	1	?	0	?	?	?	?	0	0	?	0	0	-	1	1	?	0	1	1	?	?	?
Aelosaurus colhuehuapensis	0	3	?	?	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	0	-	1	?	?	0	1	1	?	?	?
Tapuiasaurus macedoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gondwanatitan faustoi	0	3	1	0	1	2	0	1	1	?	0	?	?	?	?	1	1	?	0	0	-	1	?	?	?	?	?	?	?	?
Ampelosaurus atacis	?	3	1	?	?	1	?	?	1	0	0	?	?	?	0	0	?	?	0	?	?	?	?	?	?	?	?	?	?	?
EC1	0	3	1	2	0	1	0	?	?	?	?	?	?	?	0	0	0	1	0	0	-	1	1	?	1	1	1	?	?	?
Lirainosaurus astibiae	0	3	1	2	0	1	0	?	1	0	0	0	-	-	0	0	0	1	0	?	?	?	?	?	?	?	?	?	1	0
Diamantinasaurus matildae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Isisaurus colberti	0	3	1	2	0	0	0	1	1	0	0	?	?	?	0	0	0	0	0	0	-	1	1	?	0	1	?	?	0	0
Opisthocoelicaudia skarzynskii	0	3	1	2	0	0	0	0	2	0	0	1	0	0	?	?	0	0	?	0	-	1	1	1	1	?	0	?	0	0
Alamosaurus sanjuanensis	0	3	1	1	0	0	1	0	1	0	0	?	?	?	?	0	0	1	?	0	-	1	1	1	1	0	0	?	1	0
Saltasaurus loricatus	0	?	1	2	0	0	1	0	1	1	0	1	?	0	0	1	1	1	0	?	?	1	?	?	0	0	0	?	1	0
Neuquensaurus australis	0	3	?	2	0	0	?	0	1	1	?	1	?	0	?	1	0	1	?	?	?	?	?	?	?	?	?	?	1	0
Baurutitan britoi	0	3	1	2	0	1	0	1	?	?	?	?	?	?	0	1	0	0	0	0	-	1	1	?	?	?	0	?	?	?
Trigonosaurus pricei	0	?	?	?	?	1	?	?	?	?	?	?	?	?	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	301	302	303	304	305	306	307	308	309	310	311	312	313	314	315	316	317	318	319	320	321	322	323	324	325	326	327	328	329	330
Plateosaurus	0	0	0	0	0	0	0	0	0	?	?	0	?	0	0	?	0	0	?	?	?	1	0	0	?	-	0	0	0	0
Antetonitrus ingenipes	?	1	1	0	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	-	0	0	0	?
Vulcanodon karibaensis	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	0	1	0	?
Tazoudasaurus naimi	0	0	0	0	?	?	?	?	?	?	?	0	0	0	0	0	0	?	?	?	?	?	1	1	0	0	0	1	0	1
Barapasaurus tagorei	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	?	?	?	?	?	?	1	?	0	0	1	0	1
Shunosaurus lii	0	0	0	0	1	?	?	0	0	0	1	0	0	0	0	0	?	0	0	1	0	0	1	1	0	0	0	1	0	1
Patagosaurus fariasi	0	0	0	0	1	0	0	0	?	?	1	0	0	0	0	?	0	?	?	1	?	?	?	1	?	0	0	1	0	1
Cetiosaurus oxoniensis	0	0	0	0	0	?	?	0	?	0	1	1	0	0	?	?	?	0	0	1	0	0	?	1	0	0	0	1	0	1
Cetiosauriscus stewerti	0	?	?	?	1	0	0	0	0	?	?	0	0	0	?	?	?	?	?	?	?	?	?	1	0	0	0	1	0	1
Omeisaurus	0	0	0	0	?	?	0	0	?	?	0	0	0	0	0	0	0	0	0	?	0	0	1	1	0	?	0	1	0	1
Mamenchisaurus	0	?	?	0	?	?	?	?	?	?	1	0	?	0	0	?	?	0	?	?	?	?	1	1	?	0	0	1	0	1
Chuanjiesaurus anaensis	0	0	0	0	1	1	0	0	?	?	1	0	0	0	0	?	1	?	?	?	?	?	1	1	0	?	0	?	?	1
Bellusaurus sui	0&1	0	0	0	1	1	0	0	1	1	?	0	0	0	0	?	0	?	?	?	?	?	?	1	?	?	0	1	0	1
Lapparentosaurus madagascariensis	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	?	?	?	?	?	?	?	1	0	0	0	0/1	0	1
Jobaria tiguidensis	0	1	1	0	?	?	?	0	1	?	0	0	0	0	0	0	0	0	?	?	?	0	1	1	?	?	0	1	0	1
Losillasaurus giganteus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	1	1	1
Turiasaurus riodevensis	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	?	?	0	?	1	0	1	0	1	1	1
Zby atlanticus	?	?	?	?	?	?	?	0	1	0	0	0	0	0	0	0	0	?	?	?	?	?	?	1	0	1	0	1	1	1
Haplocanthosaurus priscus	0	2	2	1	1	0	0	0	?	?	?	1	0	0	0	0	0	?	0	0	0	?	?	?	?	?	?	?	?	?
Amazonsaurus maranhensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Zapalasaurus bonapartei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rayosaurus	0	2	1	1	0	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Histriasaurus boscarollii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rebbachisaurus	0	2	?	1	0	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Limaysaurus tessonei	0	2	1	1	0	1	1	0	1	1	1	0	0	0	0	?	1	1	1	?	?	?	1	1	?	?	0	1	0	1
Cathartesaura anaerobica	?	2	1	1	0	1	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Comahuesaurus windhauseni	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	?	?	1	?	?	?	?	?	1	?	?	0	1	0	1
Demandasaurus darwini	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nigersaurus taqueti	?	2	2	1	0	0	0	0	1	?	?	0	?	0	0	?	0	?	?	?	?	?	?	1	?	?	0	1	0	1
Dicraeosaurus	0	0	0	0	?	?	0	0	1	1	?	?	0	?	0	?	?	?	?	?	?	?	1	1	0	0	0	1	0	1
Amargasaurus cazaui	?	0	?	?	?	?	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	1	0	1
Brachytrachelopan mesai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Suuwassea emilieae	?	0	0	0	1	0	0	?	?	1	?	0	0	0	?	0	0	?	?	?	?	?	?	1	0	0	?	1	?	1
Apatosaurus	0	0	0	0	1	0	0	1	1	1	1	1	0	0	0	1	1	0	0	0	0	?	1	1	0	0	0	1	0	1
Tornieria africana	0	0	0	0	0	1	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	0	1	0	1
Supersaurus vivianae	?	0	0	0	0	1	0	?	?	1	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Barosaurus lentus	1	0	0	0	?	?	?	?	?	?	1	?	?	?	0	?	0	0	?	?	?	?	?	1	?	?	0	?	0	1
Kateedocus siberi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	301	302	303	304	305	306	307	308	309	310	311	312	313	314	315	316	317	318	319	320	321	322	323	324	325	326	327	328	329	330
Diplodocus	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1
SHN (JJS) 177	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dinheirosaurus lourinhanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Camarasaurus	0	1	0	0	1	1	0	0	1	1	1	1	0	0	0	0	1	0	0	0	?	0	1	1	0	0	0	1	0	1
Lourinhasaurus alenquerensis	0	1	0	0	1	1	0	0	1	1	1	1	0	0	0	0	1	0	?	0	?	?	1	1	0	0	0	1	0	1
SHN 181	0	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tehuelchesaurus benetezii	0	0	0	0	1	1	0	0	1	1	1	1	1	0	0	0	1	?	?	?	?	?	1	1	0	0	0	0	0	1
Aragosaurus ischiaticus	0	?	?	0	1	1	0	0	1	?	?	1	0	0	?	?	?	0	0	0	0	?	1	?	?	?	0	1	0	1
Galveosaurus herreroi	?	?	?	?	?	1	?	?	0	?	?	?	?	?	?	?	?	0	0	0	0	0	?	1	0	1	0	1	0	1
Europasaurus holgeri	0	0	0	0	1	1	0	0	1	?	1	0	0	0	0	0	1	0	0	?	?	?	?	1	?	?	0	1	0	1
Lusotitan atalaiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	1	?	?
Brachiosaurus altithorax	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	0	?	?	?	?	?	?	2	1	0	1	0	1	0	1
Giraffatitan brancai	0	1	0	0	1	0	0	0	1	1	1	0	0	0	0	?	0	0	0	0	0	0	2	1	1	1	0	1	0	1
Abydosaurus mcintoshi	?	1	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?
Venenosaurus dicrocei	?	0	0	0	1	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sonorasaurus thompsoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cedarosaurus weiskopfae	0	?	0	0	1	?	?	?	1	?	1	?	?	1	0	0	1	?	?	?	?	0	2	1	1	1	0	0	0	1
Sauroposeidon proteles	0	0	0	0	?	1	?	1	1	?	?	1	0	0	0&1	0	0	0	0	?	?	0	1	1	0	0	0	1	0	1
Tastavinsaurus sanzi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Huabeisaurus allocotus	?	0	0	0	1	0	0	?	0	1	1	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Phuwiangosaurus sirindhornae	0	0	0	0	1	0	0	1	?	1	1	1	?	?	?	?	0	1	1	?	?	?	1	1	0	?	0	1	0	1
Tangvayosaurus hoffeti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1
Yunmenglong ruyangensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Qiaowanlong kangxii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euhelopus zdanskyi	0	0	0	0	?	1	0	1	0	?	1	0	0	0	0	0	?	?	?	?	?	?	1	1	0	0	0	1	0	1
Erketu ellisoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	0	?	?	?	?	?	?	?	?	?
Daxiatitan binglingi	0	0	0	0	1	1	0	?	?	?	1	0	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Chubutisaurus insignis	1	0	0	0	1	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	1	0	1
Ligabuesaurus leanzai	1	0	0	0	1	1	0	1	1	?	?	?	?	?	?	0	?	?	?	?	?	?	1	1	0	?	0	1	0	1
Wintonotitan wattsi	?	?	?	0	?	?	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	1	?	?
Andesaurus delgadoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rukwatitan bisepultus	?	0	?	?	?	?	?	?	?	?	?	1	0	0	?	?	?	?	?	?	?	?	?	1	0	0	1	1	0	1
Mendozasaurus neguyelap	1	0	0	0	1	0	0	1	1	?	?	?	?	?	?	?	?	1	1	?	?	?	?	1	1	0	?	?	0	1
Malawisaurus dixeyi	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	1	0	1	1	0	?	1	?	1	0	?	1	1	0	1
Argentinosaurus hunculensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dreadnoughtus schrani	1	0	0	0	1	0	0	1	0	1	0	0	1	0	1	0	?	1	1	0	1	0	1	1	0	0	1	1	0	1
Epachthosaurus sciuttoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	1	0	0	1	1	?	0
Rapetosaurus krausei	1	0	0	0	?	?	0	1	?	1	?	1	0	0	0	?	0	1	?	?	?	?	?	?	0	0	0	1	1	1
Muyelensaurus pecheni	0	0	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	1	0	?	?	?	?	1

Table S.51. Data matrix

Taxa	301	302	303	304	305	306	307	308	309	310	311	312	313	314	315	316	317	318	319	320	321	322	323	324	325	326	327	328	329	330
Rinconsaurus caudamirus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	1	0	0	0	1	?	1
Overosaurus paradasorum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus rionegrinus	?	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	1	1	1
Aelosaurus maximus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?
Aelosaurus colhuehuapensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?
Tapuiasaurus macedoi	?	?	?	?	?	?	?	?	?	?	?	1	0	0	1	?	?	1	?	?	?	?	?	?	?	?	?	1	?	?
Gondwanatitan faustoi	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	0	1	1	1
Ampelosaurus atacis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	1	0	?	0	?	?	1
EC1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lirainosaurus astibiae	1	0	0	0	1	0	0	?	?	?	?	0	0	1	1	1	1	1	?	?	1	?	?	1	0	0	0	1	?	1
Diamantinasaurus matildae	?	0	?	0	?	?	?	0	1	?	?	?	?	1	?	1	1	?	?	?	?	?	?	1	0	0	0	1	1	1
Isisaurus colberti	1	0	0	0	0	0	0	1	0	?	0	0	0	0	0	0	0	?	?	?	?	1	?	1	0	0	0	1	1	1
Opisthocoelicaudia skarzynskii	0	?	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	0
Alamosaurus sanjuanensis	1	0	0	0	0	0	0	1	1	0	1	0	0	1	1	1	1	1	1	0	?	1	?	?	?	?	1	1	1	0
Saltasaurus loricatus	1	0	0	0	0	0	0	1	0	1	0	1	1	1	1	1	1	1	1	?	?	?	?	1	1	0	1	1	1	0
Neuquensaurus australis	1	0	?	0	0	0	0	1	0	?	0	1	1	1	1	?	?	1	?	?	?	?	?	1	0	0	1	1	1	0
Baurutitan britoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trigonosaurus pricei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	331	332	333	334	335	336	337	338	339	340	341	342	343	344	345	346	347	348	349	350	351	352	353	354	355	356	357	358	359	360
Plateosaurus	0	0	0	0	0	0	0	?	?	0	0	1	?	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Antetonitrus ingenipes	0	?	?	?	?	?	?	?	?	1	1	?	?	?	0	0	0	?	?	0	0	0	?	0	0	?	0	?	?	?
Vulcanodon karibaensis	0	?	?	?	?	?	0	?	?	1	1	0	0	0	1	0	0	?	1	0	?	0	?	?	?	?	?	?	?	?
Tazoudasaurus naimi	0	1	0	0	1	0	?	0	0	1	1	1	0	?	1	0	0	?	1	0	0	?	0	0	1	?	0	1	0	0
Barapasaurus tagorei	0	0	?	?	1	0	?	0	0	1	1	1	0	?	1	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?
Shunosaurus lii	0	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0
Patagosaurus fariasi	0	0	?	?	0	0	?	0	0	1	1	1	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Cetiosaurus oxoniensis	0	0	0	0	1	0	0	0	0	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cetiosauriscus stewerti	0	0	0	0	?	0	0	?	?	1	?	1	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Omeisaurus	0	0	0	0	1	?	0	?	0	1	0	1	0	1	1	0	0	0	1	0	0	0	0	?	0	1	1	1	0	0
Mamenchisaurus	0	0	?	0	1	?	0	?	?	1	0&1	1	0	?	1	0	0	1	1	0	0	1	0	0	0	1	?	?	0	0
Chuanjiesaurus anaensis	0	0	?	0	1	0	?	0	0	1	1	1	0	1	?	0	?	?	?	?	?	0	0	1	0	?	?	?	0	?
Bellusaurus sui	0	0	?	0	1	0	?	0	0	1	1	1	0	1	1	0	?	?	?	?	1	?	?	?	?	?	?	?	?	?
Lapparentosaurus madagascariensis	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	?	1	?	?	?	?	1	0	?	?	?	?	?
Jobaria tiguidensis	0	0	0	?	1	?	?	?	?	1	1	1	0	?	1	?	0	0	1	1	1	0	0	0	0	1	1	1	?	0
Losillasaurus giganteus	?	0	1	0	?	0	1	?	?	?	?	?	?	?	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Turiasaurus riodevensis	0	0	1	0	1	0	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	0	0
Zby atlanticus	0	0	1	0	1	0	1	0	1	1	1	1	0	1	1	1	1	?	?	?	?	0	0	0	0	?	?	1	0	0
Haplocanthosaurus priscus	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Amazonsaurus maranhensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Zapalasaurus bonapartei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rayosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Histriasaurus boscarollii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rebbachisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Limaysaurus tessonei	1	0	?	0	0	?	?	?	?	1	1	1	0	1	1	?	0	?	?	?	?	0	?	?	?	?	?	?	0	?
Cathartesaura anaerobica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Comahuesaurus windhauseni	1	1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Demandasaurus darwini	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nigersaurus taqueti	1	0	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dicraeosaurus	0	0	0	0	1	0	0	0	0	1	1	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Amargasaurus cazaui	0	0	?	0	1	0	?	0	0	1	0	1	0	1	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Brachytrachelopan mesai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Suuwassea emilieae	1	?	0	0	2	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apatosaurus	0	0	?	0	2	0	0	0	0	1	0	1	0	1	1	0	0	1	1	1	1	0	0	0	0	1	1	1	0	0
Tornieria africana	0	0	0	0	?	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Supersaurus vivianae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Barosaurus lentus	0	0	?	0	0	0	0	0	0	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kateedocus siberi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	331	332	333	334	335	336	337	338	339	340	341	342	343	344	345	346	347	348	349	350	351	352	353	354	355	356	357	358	359	360
Diplodocus	0	0	?	0	1	0	0	0	0	1	1	1	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
SHN (JJS) 177	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dinheirosaurus lourinhanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Camarasaurus	0	0	0	0	1	0	0	0	0	1	1	1	0	1	1	0	0	1	1	1	1	1	1	0	0	?	1	1	0	0
Lourinhasaurus alenquerensis	0	0	0	0	1	0	0	0	0	1	1	1	0	1	1	0	0	?	1	?	?	?	?	?	?	?	?	?	?	?
SHN 181	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tehuelchesaurus benetezii	0	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Aragosaurus ischiaticus	0	0	0	0	?	0	0	0	?	1	1	1	0	1	1	0	0	?	1	?	?	?	?	0	1	?	?	?	?	?
Galveosaurus herreroi	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Europasaurus holgeri	0	0	0	?	1	?	0	?	?	1	1	1	0	1	1	0	0	?	?	1	1	?	?	?	?	?	?	1	?	?
Lusotitan atalaiensis	0	?	0	0	?	?	?	0	0	1	1	1	?	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Brachiosaurus altithorax	0	0	0	0	0	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Giraffatitan brancai	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	1	1	1	1	1	1	1	1	1	0	1	0	1
Abydosaurus mcintoshi	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	1	1	1	?	?	?	?	?
Venenosaurus dicrocei	?	?	?	?	?	?	?	?	?	?	1	1	0	?	1	0	0	?	?	?	?	1	?	?	?	?	?	?	?	?
Sonorasaurus thompsoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cedarosaurus weiskopfae	0	1	1	1	0	0	0	0	0	1	1	1	?	1	?	0	0	?	?	?	?	1	?	?	?	?	?	?	?	?
Sauroposeidon proteles	1	?	1	0	0	0	?	1	0	1	1	1	0	1	1	?	0	?	?	1	?	1	?	1	1	?	?	?	?	?
Tastavinsaurus sanzi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Huabeisaurus allocotus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Phuwiangosaurus sirindhornae	1	0	0	0	0	0	0	0	?	1	1	1	1	1	1	1	0	?	?	1	?	?	?	?	?	?	?	?	?	?
Tangvayosaurus hoffeti	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?
Yunmenglong ruyangensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Qiaowanlong kangxii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euhelopus zdanskyi	1	0	1	0	1	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Erketu ellisoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Daxiatitan binglingi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chubutisaurus insignis	1	1	?	0	0	0	0	1	0	1	?	?	?	?	1	1	0	?	?	1	1	1	1	1	1	?	?	?	?	?
Ligabuesaurus leanzai	1	1	0	0	0	0	?	1	0	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?
Wintonotitan wattsi	?	0	1	0	?	?	0	?	?	?	1	1	0	1	?	1	1	1	?	1	1	1	?	?	?	?	?	?	?	?	?
Andesaurus delgadoi	?	?	?	?	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rukwatitan bisepultus	1	1	1	0	1	0	?	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mendozasaurus neguyelap	1	0	?	?	1	0	1	0	0	1	?	?	0	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?
Malawisaurus dixeyi	1	1	1	0	1	0	1	1	0	1	0	0	0	?	?	?	0	?	?	1	?	?	1	1	1	?	?	?	0	?
Argentinosaurus hunculensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dreadnoughtus schrani	1	0	1	1	1	0	1	0	0	1	0	0	0	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Epachthosaurus sciuttoi	1	0	1	1	1	0	?	1	0	1	?	0	0	0	?	1	1	?	?	1	1	1	?	1	2	?	?	1	?	?
Rapetosaurus krausei	1	0	1	0	0	0	1	0	0	1	1	1	0	1	1	1	0	?	?	?	?	?	?	1	?	?	?	?	0	?
Muyelensaurus pecheni	1	1	?	0	0	0	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	331	332	333	334	335	336	337	338	339	340	341	342	343	344	345	346	347	348	349	350	351	352	353	354	355	356	357	358	359	360
Rinconsaurus caudamirus	?	0	?	0	?	0	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Overosaurus paradasorum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus rionegrinus	?	?	?	?	?	?	?	?	?	1	?	0	1	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?
Aelosaurus maximus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus colhuehuapensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapuiasaurus macedoi	?	?	?	?	?	?	?	?	?	?	1	0	0	?	?	1	?	?	?	?	?	1	?	?	?	?	?	?	?	?
Gondwanatitan faustoi	1	?	?	0	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ampelosaurus atacis	1	0	?	0	1	0	?	0	0	1	?	0	0	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
EC1	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lirainosaurus astibiae	1	0	1	0	0	0	1	0	0	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Diamantinasaurus matildae	1	0	1	0	2	0	1	1	0	1	1	0	1	0	1	1	1	1	?	1	1	1	1	1	0	1	?	1	0	1
Isisaurus colberti	1	0	?	0	1	0	1	0	0	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Opisthocoelicaudia skarzynskii	1	1	1	1	2	1	1	1	0	1	1	0	1	0	1	1	1	1	?	1	1	1	1	1	1	2	?	?	1	1
Alamosaurus sanjuanensis	1	0	1	0	0	0	1	0	0	1	1	0	0	0	1	1	1	1	?	1	1	1	1	1	1	2	?	?	1	1
Saltasaurus loricatus	1	0	1	1	2	1	1	1	0	1	1	0	1	0	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Neuquensaurus australis	1	0	1	1	2	1	1	1	0	1	1	0	1	0	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Baurutitan britoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trigonosaurus pricei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	361	362	363	364	365	366	367	368	369	370	371	372	373	374	375	376	377	378	379	380	381	382	383	384	385	386	387	388	389	390
Plateosaurus	0	0	?	?	?	0	0	0	0	0	0	0	?	?	0	?	?	?	0	?	0	0	0	0	0	0	0	0	0	?
Antetonitrus ingenipes	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Vulcanodon karibaensis	1	1	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	?	0	?	0	?
Tazoudasaurus naimi	1	1	0	0	0	1	?	?	0	0	?	0	0	?	0	?	?	0	?	0	0	0	?	0	1	0	0	0	0	?
Barapasaurus tagorei	?	?	?	?	?	1	1	0	0	0	0	0	0	?	0	?	0	0	?	0	1	0	?	0	?	0	0	0	0	?
Shunosaurus lii	1	1	?	0	0	1	1	0	0	0	0	0	?	0	0	0	0	?	0	0	1	0	1	0	0	?	0	0	0	0
Patagosaurus fariasi	?	?	?	?	?	1	1	0	0	0	0	?	?	?	0	?	0	?	?	0	1	0	1	0	?	0	0	?	0	?
Cetiosaurus oxoniensis	1	1	?	?	?	1	?	0	0	0	0	?	?	?	?	?	0	?	?	0	?	0	1	0	?	?	0	?	0	0
Cetiosauriscus stewerti	?	?	?	?	?	1	1	0	0	0	0	?	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Omeisaurus	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	?
Mamenchisaurus	?	?	?	0	0	1	1	0	0	0	0	?	?	?	0	0	?	0	0	0	?	?	?	0	0	0	0	0	0	?
Chuanjiesaurus anaensis	1	?	?	?	?	1	1	0	0	0	0	?	0	?	0	?	0	0	0	?	?	0	?	0	0	0	?	0	?	?
Bellusaurus sui	?	?	?	?	?	1	1	0	0	0	0	?	?	?	?	?	0	?	?	1	1	1	1	0	?	1	1	0	0	?
Lapparentosaurus madagascariensis	?	1	?	1	0	1	1	0	0	0	0	?	0	0	0	0	0	0	?	1	1	0	1	0	0	0	1	0	0	0
Jobaria tiguidensis	1	?	0	?	?	1	?	0	0	0	0	1	?	0	1	?	?	?	?	0	1	0	?	?	?	0	1	?	0	?
Losillasaurus giganteus	?	?	?	?	?	?	1	?	0	0	?	?	?	?	?	0	?	?	?	0	1	0	?	?	?	0	1	?	0	0
Turiasaurus riodevensis	1	1	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Zby atlanticus	?	1	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Haplocanthosaurus priscus	?	?	?	?	?	1	1	0	0	0	0	1	1	?	1	?	0	0	0	1	1	0	1	0	0	0	1	0	0	?
Amazonsaurus maranhensis	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Zapalasaurus bonapartei	?	?	?	?	?	1	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	0	1	0	?	?
Rayosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Histriasaurus boscarollii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rebbachisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Limaysaurus tessonei	1	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0	1	0	0	0	1	0	0	?
Cathartesaura anaerobica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Comahuesaurus windhauseni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	0	?	0	1	?	0	?
Demandasaurus darwini	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	?
Nigersaurus taqueti	?	?	?	?	1	1	1	0	?	?	0	?	?	?	?	0	?	?	0	?	?	?	?	?	?	?	?	?	1	?
Dicraeosaurus	?	?	?	?	?	1	1	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0	?
Amargasaurus cazaui	?	?	?	?	?	1	1	0	0	0	1	?	?	?	1	?	?	0	?	?	?	?	1	?	?	?	?	?	?	?
Brachytrachelopan mesai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Suuwassea emilieae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apatosaurus	1	1	?	0	0	1	1	0	0	0	0	1	?	?	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0
Tornieria africana	?	?	?	?	?	?	1	0	0	0	?	?	0	0	1	0	0	0	?	?	?	?	?	0	0	0	0	1	0	?
Supersaurus vivianae	?	?	?	?	?	1	1	0	0	0	?	1	?	?	1	?	0	0	0	1	1	0	1	0	0	0	0	1	0	?
Barosaurus lentus	?	?	?	?	?	1	1	0	0	0	0	1	0	?	1	?	0	?	0	1	1	0	1	0	?	?	0	1	0	?
Kateedocus siberi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

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Taxa	361	362	363	364	365	366	367	368	369	370	371	372	373	374	375	376	377	378	379	380	381	382	383	384	385	386	387	388	389	390
Diplodocus	?	?	?	0	0	1	1	0	0	0	0	1	0	?	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0
SHN (JJS) 177	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	0	1	0	1	0	0	0	0	1	0	0
Dinheirosaurus lourinhanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Camarasaurus	1	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0
Lourinhasaurus alenquerensis	?	?	?	?	?	1	1	0	0	0	0	?	0	0	0	0	0	?	0	0	1	?	1	0	0	1	1	0	0	0
SHN 181	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	1	0	1	?	1	?	?	?	1	0	0	1
Tehuelchesaurus benetezii	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	1	1	0	0	1	1	0	0	0
Aragosaurus ischiaticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	1	0	0	1	1	0	0	0
Galveosaurus herreroi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	1
Europasaurus holgeri	1	1	0	?	1	1	1	1	0	0	1	1	1	0	?	?	?	0	?	0	1	1	?	0	?	?	1	0	0	?
Lusotitan atalaiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	0	0	1	?	?	0	1
Brachiosaurus altithorax	?	?	?	?	?	?	?	1	0	0	1	?	1	?	0	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?
Giraffatitan brancai	1	1	?	1	1	1	1	1	0	0	1	1	1	1	0	0	1	?	1	0	1	1	1	0	1	1	1	0	0	1
Abydosaurus mcintoshi	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Venenosaurus dicrocei	?	?	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	?	1	0	1	1	?	0	0	?
Sonorasaurus thompsoni	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cedarosaurus weiskopfae	?	?	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sauroposeidon proteles	?	?	0	0	1	?	?	?	0	?	?	1	1	0	?	?	?	?	1	0	1	1	?	0	1	1	1	0	0	1
Tastavinsaurus sanzi	?	?	?	?	?	1	1	1	0	0	1	1	1	0	1	0	1	0	1	0	1	1	1	0	1	1	1	0	0	1
Huabeisaurus allocotus	?	?	?	?	?	1	1	1	0	0	1	?	?	0	1	?	?	?	1	0	1	0	1	0	1	1	1	0	1	1
Phuwiangosaurus sirindhornae	?	?	0	?	1	1	1	1	0	0	1	?	1	0	1	?	0	0	1	0	1	1	1	1	-	?	1	0	0	1
Tangvayosaurus hoffeti	?	?	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1	?	1	-	1	1	0	?	?
Yunmenglong ruyangensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Qiaowanlong kangxii	?	?	?	?	?	1	1	1	0	0	1	?	1	0	1	?	0	0	1	0	?	0	1	0	1	1	?	0	?	?
Euhelopus zdanskyi	?	?	?	?	?	1	1	1	0	0	1	1	1	?	1	1	0	?	0	0	1	0	1	0	0	1	1	0	0	1
Erketu ellisoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Daxiatitan binglingi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chubutisaurus insignis	?	?	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	1	0	0	?
Ligabuesaurus leanzai	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Wintonotitan wattsi	1	?	0	0	1	?	?	?	?	?	?	?	1	?	?	0	?	?	?	?	?	?	?	1	-	1	?	0	0	1
Andesaurus delgadoi	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1	?	1	-	1	1	0	0	1
Rukwatitan bisepultus	?	?	?	?	?	1	1	1	0	0	?	?	1	?	1	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?
Mendozasaurus neguyelap	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Malawisaurus dixeyi	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	-	1	1	0	0	1
Argentinosaurus hunculensis	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dreadnoughtus schrani	?	?	?	?	?	1	?	?	?	1	?	1	1	1	1	1	?	0	1	0	1	0	1	1	-	1	1	0	0	1
Epachthosaurus sciuttoi	1	?	0	0	1	1	?	1	1	1	?	1	1	?	?	1	?	?	1	?	1	?	?	1	-	?	?	?	0	?
Rapetosaurus krausei	?	?	?	1	1	1	1	1	0	0	1	1	?	?	1	?	0	0	1	0	1	1	1	1	-	1	1	0	0	1
Muyelensaurus pecheni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1	?	1	-	?	?	?	?	?

Table S.51. Data matrix

Taxa	361	362	363	364	365	366	367	368	369	370	371	372	373	374	375	376	377	378	379	380	381	382	383	384	385	386	387	388	389	390
Rinconsaurus caudamirus	?	?	?	?	?	1	1	1	0	0	1	?	?	1	?	?	1	?	?	?	?	?	?	1	-	1	?	0	?	?
Overosaurus paradasorum	?	?	?	?	?	1	1	0	0	0	1	1	?	?	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus rionegrinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus maximus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus colhuehuapensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapuiasaurus macedoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gondwanatitan faustoi	?	?	?	?	?	?	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ampelosaurus atacis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	1	-	1	1	0	?	?
EC1	?	?	?	?	?	1	1	1	1	1	1	1	1	?	1	1	?	0	1	?	1	?	?	1	-	1	1	0	0	1
Lirainosaurus astibiae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	0	?	?	?	?	?	?	?	?	?	?
Diamantinasaurus matildae	1	1	0	0	0	1	1	1	1	1	1	?	1	0	0	1	1	1	1	0	1	1	1	1	-	1	1	0	?	1
Isisaurus colberti	?	?	?	?	?	1	0	1	1	1	1	1	1	?	1	?	1	?	1	0	1	1	1	0	1	1	1	0	0	?
Opisthocoelicaudia skarzynskii	1	1	0	0	1	1	1	1	1	1	1	1	?	?	1	?	0	1	1	0	1	0	1	1	-	?	1	0	0	1
Alamosaurus sanjuanensis	1	1	0	0	0	?	?	?	?	?	1	?	1	1	1	1	?	?	?	?	?	0	?	1	-	1	1	0	?	1
Saltasaurus loricatus	?	?	0	?	?	1	1	1	1	1	1	1	1	1	1	1	?	0	1	0	1	1	1	1	-	1	1	0	0	1
Neuquensaurus australis	?	?	?	?	1	1	1	1	1	?	?	?	?	?	?	?	?	?	1	0	1	?	?	1	-	1	1	0	0	1
Baurutitan britoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trigonosaurus pricei	?	?	?	?	?	1	1	1	1	1	?	1	1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	391	392	393	394	395	396	397	398	399	400	401	402	403	404	405	406	407	408	409	410	411	412	413	414	415	416	417	418	419	420
Plateosaurus	?	0	0	?	?	0	?	0	0	?	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0
Antetonitrus ingenipes	?	?	?	?	?	?	?	0	?	1	0	?	?	?	?	0	?	1	0	0	0	?	0	?	0	0	?	?	0	?
Vulcanodon karibaensis	0	?	0	0	0	1	0	1	1	1	0	?	?	?	?	0	1	1	?	?	?	0	0	0	0	0	0	1	0	0
Tazoudasaurus naimi	0	?	0	0	?	1	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0
Barapasaurus tagorei	0	?	0	0	?	1	0	1	1	1	0	0	0	1	0	1	1	1	1	0	0	1	0	0	0	0	?	1	1	1
Shunosaurus lii	?	0	0	0	0	?	0	1	1	0	0	0	1	0	0	1	1	1	1	0	0	?	0	0	0	0	?	1	1	1
Patagosaurus fariasi	0	0	0	0	?	1	?	1	1	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	?	?	0	?
Cetiosaurus oxoniensis	0	0	0	0	?	?	0	1	1	1	0	1	1	0	0	1	1	1	1	0	?	1	0	0	0	1	0	1	0	1
Cetiosauriscus stewerti	?	?	?	?	?	?	?	1	1	1	0	0	0	?	?	1	1	1	?	0	0	1	0	?	?	0	?	?	?	?
Omeisaurus	0	0	0	0	0	1	0	1	1	0	0	?	?	0	0	1	1	1	0	0	0	0	?	0	0	0	0	?	1	1
Mamenchisaurus	?	0	0	0	0	1	0	1	1	0	0	0	1	0	0	1	1	1	1	0	0	?	0	0	0	0	?	1	1	?
Chuanjiesaurus anaensis	?	?	?	0	0	?	?	1	1	0	0	1	1	0	0	1	1	?	1	0	0	1	0	0	0	?	?	0	1	1
Bellusaurus sui	0	?	0	0	?	1	0	?	1	0	0	0	0	0	?	1	1	?	1	0	?	?	?	?	0	0	?	0	1	1
Lapparentosaurus madagascariensis	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	1	1	1	1	0	0	1	0	0	1	0	1	?	1	1
Jobaria tiguidensis	0	?	0	0	?	1	?	1	1	?	?	?	?	?	?	1	1	1	1	0	0	?	?	?	?	0	?	0	1	1
Losillasaurus giganteus	0	?	0	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Turiasaurus riodevensis	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	0	1
Zby atlanticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Haplocanthosaurus priscus	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	1	1	1	1	1	0	?	0	?	?	?	?	?	?	1
Amazonsaurus maranhensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Zapalasaurus bonapartei	?	?	0	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?
Rayosaurus	?	?	?	?	?	?	?	2	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?
Histriasaurus boscarollii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rebbachisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Limaysaurus tessonei	0	0	1	0	0	1	0	2	1	?	1	1	0	1	0	1	1	1	?	0	0	?	0	0	?	0	?	?	1	?
Cathartesaura anaerobica	?	?	?	?	?	?	?	2	?	?	0	1	?	?	?	1	?	1	1	?	?	?	0	?	?	?	?	?	?	?
Comahuesaurus windhauseni	?	?	1	0	?	1	?	2	1	1	0	0	1	0	1	1	1	?	1	0	0	1	0	0	?	?	?	?	?	?
Demandasaurus darwini	1	0	1	0	0	1	0	?	1	1	0	0	0	1	0	1	1	?	?	0	0	1	1	0	?	?	?	?	?	?
Nigersaurus taqueti	?	?	1	?	?	?	?	2	0	?	?	?	?	?	?	?	?	?	?	?	0	?	1	0	?	?	?	?	?	?
Dicraeosaurus	0	0	0	?	0	0	0	1	1	1	0	0	1	0	0	1	1	1	1	0	0	1	0	0	1	0	1	?	1	1
Amargasaurus cazaui	?	?	?	?	?	?	?	1	1	1	0	?	0	?	?	1	1	1	?	0	0	?	?	?	?	?	?	?	?	?
Brachytrachelopan mesai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Suuwassea emilieae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	?	?	1
Apatosaurus	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	1	0	0	0	1	1
Tornieria africana	0	0	0	0	0	0	0	?	?	1	0	0	1	0	0	1	1	?	1	0	1	?	0	0	1	0	1	?	?	1
Supersaurus vivianae	0	?	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	?	1	?
Barosaurus lentus	0	?	0	0	0	0	0	1	1	1	0	1	1	0	0	1	1	1	1	0	?	?	0	?	?	0	?	0	?	1
Kateedocus siberi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	391	392	393	394	395	396	397	398	399	400	401	402	403	404	405	406	407	408	409	410	411	412	413	414	415	416	417	418	419	420
Diplodocus	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	1	1	1	?	0	1	1	0	0	1	0	1	0	1	1
SHN (JJS) 177	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dinheirosaurus lourinhanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Camarasaurus	0	0	0	0	0	1	1	1	1	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	1	0	1	0	1	1
Lourinhasaurus alenquerensis	0	0	0	0	0	1	1	1	1	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	1	0	1	0	1	?
SHN 181	?	0	?	0	?	1	?	1	1	0	?	?	0	?	?	?	1	?	?	?	0	1	0	0	?	0	0	?	1	1
Tehuelchesaurus benetezii	0	0	0	0	0	1	0	1	1	1	1	0	0	1	1	1	1	1	0	0	0	1	0	0	?	?	?	?	?	?
Aragosaurus ischiaticus	0	0	0	0	0	1	0	1	1	1	1	0	0	1	1	1	1	1	1	0	0	1	0	0	?	?	?	?	?	?
Galveosaurus herreroi	0	?	?	0	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Europasaurus holgeri	0	0	0	0	?	1	?	1	1	1	0	0	0	1	?	1	1	1	1	0	0	1	?	0	1	0	0	?	1	1
Lusotitan atalaiensis	0	0	0	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	?	1	1
Brachiosaurus altithorax	?	?	?	?	?	?	?	1	1	1	1	0	0	1	1	1	1	2	1	0	0	?	0	0	?	?	?	?	?	?
Giraffatitan brancai	0	0	0	0	0	1	0	1	1	1	1	1	0	1	1	1	1	2	1	0	0	1	1	0	1	0	1	1	1	1
Abydosaurus mcintoshi	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?
Venenosaurus dicrocei	0	?	0	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sonorasaurus thompsoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cedarosaurus weiskopfae	?	?	?	?	?	?	0	1	1	1	1	?	?	?	?	1	?	2	1	0	?	?	1	0	?	0	?	?	?	?
Sauroposeidon proteles	0	?	?	0	0	1	0	1	1	1	1	1	0	1	0	1	1	2	1	0	0	1	1	0	0	0	0	?	1	1
Tastavinsaurus sanzi	0	0	0	0	1	1	0	1	1	1	1	0	0	1	0	1	1	1	1	0	0	1	1	0	1	0	1	1	1	1
Huabeisaurus allocotus	0	1	?	0	1	1	0	1	1	1	1	?	0	?	1	?	1	1	?	0	0	1	1	0	?	0	0	0	1	?
Phuwiangosaurus sirindhornae	0	?	0	0	?	1	0	1	0	1	1	1	0	1	1	1	1	2	1	0	0	1	1	0	1	1	0	?	1	1
Tangvayosaurus hoffeti	0	?	?	0	1	1	0	1	?	?	1	1	0	?	1	1	1	2	?	0	?	?	?	0	?	0	?	?	?	1
Yunmenglong ruyangensis	?	?	?	?	?	?	?	1	?	1	1	1	0	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Qiaowanlong kangxii	0	?	?	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euhelopus zdanskyi	0	1	0	0	0	1	0	1	0	0	1	0	1	0	1	1	1	1	1	0	0	1	1	0	1	0	0	0	1	1
Erketu ellisoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	1	1
Daxiatitan binglingi	?	?	?	?	?	?	?	1	?	?	1	0	1	0	1	1	1	?	?	0	?	?	?	?	?	?	?	?	?	?
Chubutisaurus insignis	0	?	?	0	?	1	0	1	?	1	1	?	?	?	?	1	?	2	1	0	0	?	?	0	1	0	1	?	1	?
Ligabuesaurus leanzai	?	?	?	?	?	?	?	1	?	1	1	1	0	1	?	1	1	2	1	0	0	?	1	0	1	0	?	?	1	1
Wintonotitan wattsi	0	?	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Andesaurus delgadoi	0	?	0	0	1	?	0	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rukwatitan bisepultus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mendozasaurus neguyelap	?	?	?	?	?	?	?	1	?	?	1	?	?	?	?	1	?	2	?	?	?	?	?	?	?	0	?	?	1	?
Malawisaurus dixeyi	0	?	?	0	1	1	0	?	?	1	1	?	?	?	?	1	?	2	?	?	?	?	1	0	?	?	?	?	1	1
Argentinosaurus hunculensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
Dreadnoughtus schrani	0	1	0	1	1	1	0	1	1	1	1	1	0	1	1	1	1	2	1	1	0	1	1	0	0	1	0	1	1	1
Epachthosaurus sciuttoi	?	?	?	1	?	?	?	1	?	1	1	?	0	?	?	1	1	2	1	1	0	?	?	?	?	0	?	?	?	1
Rapetosaurus krausei	0	?	0	1	1	1	0	1	1	1	1	1	0	1	0	1	1	?	1	1	0	1	1	0	0	?	0	?	1	1
Muyelensaurus pecheni	1	1	?	0	1	?	?	1	?	?	1	?	?	?	?	1	?	?	1	?	?	?	?	?	?	?	?	?	1	?

Table S.51. Data matrix

Taxa	391	392	393	394	395	396	397	398	399	400	401	402	403	404	405	406	407	408	409	410	411	412	413	414	415	416	417	418	419	420
Rinconsaurus caudamirus	?	?	?	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Overosaurus paradasorum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus rionegrinus	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus maximus	?	?	?	?	?	?	?	1	?	1	1	?	?	?	0	1	1	2	?	0	?	1	?	?	?	?	?	?	?	?
Aelosaurus colhuehuapensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapuiasaurus macedoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	1
Gondwanatitan faustoi	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?	?
Ampelosaurus atacis	1	?	?	1	1	1	0	1	1	1	1	1	0	1	1	1	1	2	1	1	0	1	1	0	1	?	?	0	1	1
EC1	1	1	0	1	1	1	0	1	1	1	1	1	0	1	?	1	1	1	1	1	0	1	1	0	1	?	?	0	1	1
Lirainosaurus astibiae	?	?	?	?	?	?	?	1	1	1	1	1	0	1	0	1	1	2	1	1	0	1	1	0	0	1	0	?	?	1
Diamantinasaurus matildae	1	1	0	1	1	1	0	1	1	1	1	0	0	1	?	1	1	2	1	1	0	1	1	1	1	1	1	1	0	1
Isisaurus colberti	1	?	0	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Opisthocoelicaudia skarzynskii	1	1	?	0	0	1	0	1	1	1	1	0	0	1	1	1	1	2	1	1	0	1	0	0	0	1	1	1	1	1
Alamosaurus sanjuanensis	1	1	0	1	1	1	0	?	1	1	1	?	?	?	?	?	1	2	1	1	1	?	1	1	?	1	?	?	1	1
Saltasaurus loricatus	1	?	0	1	1	1	0	1	1	1	1	1	0	1	1	1	1	2	1	1	1	1	1	1	1	1	?	?	1	1
Neuquensaurus australis	1	?	0	1	1	1	0	1	1	1	1	1	0	1	1	1	1	2	1	1	1	?	1	1	1	1	0	?	1	1
Baurutitan britoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trigonosaurus pricei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	421	422	423	424	425	426	427	428	429	430	431	432	433	434	435	436	437	438	439	440	441	442	443	444	445	446	447	448	449	450
Plateosaurus	0	?	?	0	0	?	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	?	?
Antetonitrus ingenipes	0	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	?	1	?	0	0	?	?
Vulcanodon karibaensis	0	?	?	0	0	?	?	1	0	1	0	0	0	0	0	0	?	0	1	1	0	?	1	0	0	1	0	0	?	?
Tazoudasaurus naimi	1	0	0	0	0	?	0	1	0	1	0	0	?	1	0	0	?	0	?	1	0	0	?	0	1	1	?	0	0	0
Barapasaurus tagorei	1	0	?	0	1	?	0	1	0	?	?	0	?	1	?	?	?	0	?	1	1	0	1	0	?	?	?	?	0	?
Shunosaurus lii	1	0	0	0	0	0	?	1	0	0	?	0	?	1	?	0	0	0	1	1	1	1	1	0	1	1	1	0	0	0
Patagosaurus fariasi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	1	1	?	?	?	?
Cetiosaurus oxoniensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cetiosauriscus stewerti	?	0	0	0	0	0	0	1	?	?	?	?	0	?	?	1	?	?	?	?	1	1	1	1	1	1	?	?	0	0
Omeisaurus	1	?	0	0	0	0	?	1	0	0	?	0	0	1	0	0	?	0	?	1	1	1	1	1	1	1	1	1	0	0
Mamenchisaurus	1	?	?	0	1	0	0	1	0	0	0	0	0	1	0	1	?	?	?	1	1	1	1	0	1	?	1	1	?	?
Chuanjiesaurus anaensis	1	?	?	0	0	?	?	?	0	?	?	0	0	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bellusaurus sui	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lapparentosaurus madagascariensis	?	?	?	?	0	0	0	1	1	1	0	0	1	1	0	1	?	?	?	?	?	1	1	0	1	?	?	?	?	?
Jobaria tiguidensis	1	?	?	?	0	0	?	1	1	?	?	0	?	1	1	1	0	0	?	1	1	1	1	0	1	1	1	1	?	0
Losillasaurus giganteus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Turiasaurus riodevensis	1	?	0	0	?	?	?	1	1	1	1	0	1	1	0	0	0	?	?	1	1	?	?	?	1	1	?	?	0	?
Zby atlanticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Haplocanthosaurus priscus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Amazonsaurus maranhensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Zapalasaurus bonapartei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rayosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Histriasaurus boscarollii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rebbachisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Limaysaurus tessonei	1	?	?	0	?	?	?	?	1	?	?	0	1	?	?	?	?	?	?	?	1	0	0	0	1	1	1	1	?	?
Cathartesaura anaerobica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Comahuesaurus windhauseni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Demandasaurus darwini	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nigersaurus taqueti	?	?	?	0	?	0	?	?	1	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dicraeosaurus	1	0	0	0	0	?	0	1	1	1	0	0	1	1	1	1	0	?	?	?	1	1	1	1	1	1	?	1	?	?
Amargasaurus cazaui	?	?	?	?	?	?	?	?	1	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Brachytrachelopan mesai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Suuwassea emilieae	1	0	0	0	0	0	0	1	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	0
Apatosaurus	1	1	0	0	0	?	?	1	1	1	?	0	1	1	1	1	?	1	?	1	1	1	1	1	1	1	1	1	0	0
Tornieria africana	1	0	0	0	?	?	0	1	1	1	0	0	?	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Supersaurus vivianae	1	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Barosaurus lentus	?	?	0	0	0	?	?	1	1	?	?	0	?	1	1	1	0	?	?	?	?	?	?	1	?	1	?	?	?	?
Kateedocus siberi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	421	422	423	424	425	426	427	428	429	430	431	432	433	434	435	436	437	438	439	440	441	442	443	444	445	446	447	448	449	450
Diplodocus	1	0	0	0	0	1	1	1	1	1	1	0	1	1	1	1	?	0	?	1	1	1	1	1	1	1	1	1	?	?
SHN (JJS) 177	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dinheirosaurus lourinhanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Camarasaurus	1	0	0	0&1	0	0	0	1	1	1	1	0	1	1	0	1	0	0	1	1	1	1	1	0	1	1	1	1	0	0
Lourinhasaurus alenquerensis	1	0	0	0	0	0	?	1	1	1	?	0	1	1	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
SHN 181	1	0	0	1	0	0	0	1	1	1	1	0	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Tehuelchesaurus benetezii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aragosaurus ischiaticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Galveosaurus herreroi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Europasaurus holgeri	1	?	0	0	0	0	?	1	1	1	?	0	1	1	0	1	?	?	?	1	1	?	1	?	?	?	1	?	?	?
Lusotitan atalaiensis	1	?	?	?	?	0	0	1	1	1	1	0	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Brachiosaurus altithorax	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Giraffatitan brancai	1	0	0	0	0	0	0	1	1	1	1	0	1	1	0	1	0	0	?	1	1	1	1	0	1	1	1	?	0	1
Abydosaurus mcintoshi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Venenosaurus dicrocei	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	1	1
Sonorasaurus thompsoni	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1
Cedarosaurus weiskopfae	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	1	?	?	?	1	?
Sauroposeidon proteles	1	0	1	1	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tastavinsaurus sanzi	1	0	0	1	1	1	1	1	1	1	0	0	1	0	0	1	1	0	1	1	1	1	1	0	1	1	0	1	1	0
Huabeisaurus allocotus	1	1	1	1	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Phuwiangosaurus sirindhornae	1	0	0	1	0	1	0	1	?	?	?	?	1	?	?	?	?	?	?	?	?	1	1	1	?	?	?	?	?	?
Tangvayosaurus hoffeti	1	0	?	0	0	1	?	1	1	?	?	0	?	0	?	1	1	?	?	?	?	1	0	0	1	1	1	1	?	?
Yunmenglong ruyangensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Qiaowanlong kangxii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euhelopus zdanskyi	1	1	0	1	0	1	0	1	1	1	0	0	1	?	?	1	1	0	?	1	1	1	1	?	1	?	1	1	0	0
Erketu ellisoni	1	1	1	1	0	1	?	?	1	?	?	?	?	1	?	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?
Daxiatitan binglingi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chubutisaurus insignis	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	0
Ligabuesaurus leanzai	1	0	?	0	0	0	?	?	1	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	1	0
Wintonotitan wattsi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Andesaurus delgadoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rukwatitan bisepultus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mendozasaurus neguyelap	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	?	?	?
Malawisaurus dixeyi	1	?	?	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	0	?
Argentinosaurus hunculensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dreadnoughtus schrani	1	1	?	1	0	1	1	1	1	1	0	1	1	0	0	1	?	?	?	?	1	1	1	0	?	?	?	?	?	?
Epachthosaurus sciuttoi	1	?	1	1	0	?	?	?	1	1	0	1	?	0	?	1	1	1	?	?	1	1	1	0	1	1	1	1	?	0
Rapetosaurus krausei	1	0	1	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0
Muyelensaurus pecheni	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	421	422	423	424	425	426	427	428	429	430	431	432	433	434	435	436	437	438	439	440	441	442	443	444	445	446	447	448	449	450
Rinconsaurus caudamirus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Overosaurus paradasorum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus rionegrinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus maximus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Aelosaurus colhuehuapensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tapuiasaurus macedoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gondwanatitan faustoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ampelosaurus atacis	1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
EC1	1	0	0	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lirainosaurus astibiae	1	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Diamantinasaurus matildae	1	0	1	0	0	1	0	1	1	1	0	1	1	0	0	1	1	?	?	?	?	?	?	?	1	?	?	?	?	?
Isisaurus colberti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Opisthocoelicaudia skarzynskii	1	0	1	1	0	1	?	1	1	1	0	1	1	0	0	1	1	1	-	1	1	1	1	0	1	1	1	1	0	0
Alamosaurus sanjuanensis	1	0	?	1	1	1	1	?	?	?	?	?	?	?	?	?	1	?	?	1	?	?	?	?	?	?	?	?	1	0
Saltasaurus loricatus	1	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Neuquensaurus australis	1	1	0	1	0	1	0	1	1	?	?	1	?	0	0	1	?	?	?	?	1	1	1	0	?	?	?	?	?	0
Baurutitan britoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trigonosaurus pricei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	451	452	453	454	455	456	457	458	459	460	461	462	463	464
Plateosaurus	0	0	0	0	0	0	0	0	0	0	0	0	-	0
Antetonitrus ingenipes	0	?	?	?	?	?	?	?	?	?	?	0	-	?
Vulcanodon karibaensis	1	0	0	?	0	1	1	0	0	1	0	0	-	1
Tazoudasaurus naimi	?	0	0	0	1	0	1	0	?	1	?	0	-	1
Barapasaurus tagorei	?	?	?	1	?	?	1	?	?	0	?	0	-	1
Shunosaurus lii	1	1	1	?	1	1	1	1	1	0	0	0	-	1
Patagosaurus fariasi	?	?	?	?	?	?	?	?	?	?	?	0	-	1
Cetiosaurus oxoniensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cetiosauriscus stewerti	1	1	1	1	?	1	1	?	?	?	0	0	-	1
Omeisaurus	1	1	1	1	1	1	1	1	1	0	0	0	-	1
Mamenchisaurus	1	1	1	1	?	?	1	?	?	?	?	0	-	1
Chuanjiesaurus anaensis	?	?	?	?	?	?	?	?	?	?	?	0	-	1
Bellusaurus sui	?	?	?	?	?	?	?	?	?	?	?	0	-	1
Lapparentosaurus madagascariensis	?	1	?	?	?	?	?	?	?	?	?	?	?	?
Jobaria tiguidensis	1	?	?	?	?	?	?	?	?	?	?	0	-	1
Losillasaurus giganteus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Turiasaurus riodevensis	?	1	1	1	0	?	1	1	1	?	0	?	?	1
Zby atlanticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Haplocanthosaurus priscus	?	?	?	?	?	?	?	?	?	?	?	0	-	1
Amazonsaurus maranhensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Zapalasaurus bonapartei	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rayosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Histriasaurus boscarollii	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rebbachisaurus	?	?	?	?	?	?	?	?	?	?	?	0	-	1
Limaysaurus tessonei	?	?	?	?	?	?	?	?	?	?	?	0	-	1
Cathartesaura anaerobica	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Comahuesaurus windhauseni	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Demandasaurus darwini	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nigersaurus taqueti	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Dicraeosaurus	1	?	?	?	?	1	1	?	?	?	?	0	-	1
Amargasaurus cazaui	?	?	?	?	?	?	?	?	?	?	?	0	-	1
Brachytrachelopan mesai	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Suuwassea emilieae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apatosaurus	?	1	1	1	1	?	1	1	1	0	1	0	-	1
Tornieria africana	?	?	?	?	?	?	?	?	?	?	?	0	-	?
Supersaurus vivianae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Barosaurus lentus	?	?	?	?	?	?	?	?	?	?	?	0	-	1
Kateedocus siberi	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

Taxa	451	452	453	454	455	456	457	458	459	460	461	462	463	464
Diplodocus	1	1	1	1	?	1	1	1	1	0	1	0	-	1
SHN (JJS) 177	?	?	?	?	?	?	?	?	?	?	?	0	-	1
Dinheirosaurus lourinhanensis	?	?	?	?	?	?	?	?	?	?	?	0	-	?
Camarasaurus	1	1	1	1	1	1	1	1	1	0	0	0	-	1
Lourinhasaurus alenquerensis	?	?	?	?	?	?	?	?	?	?	?	0	-	1
SHN 181	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tehuelchesaurus benetezii	?	?	?	?	?	?	?	?	?	?	?	0	-	1
Aragosaurus ischiaticus	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Galveosaurus herreroi	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Europasaurus holgeri	?	1	?	1	?	?	1	1	?	?	?	0	-	1
Lusotitan atalaiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Brachiosaurus altithorax	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Giraffatitan brancai	1	1	1	1	?	?	1	1	?	0	0	0	-	1
Abydosaurus mcintoshi	?	?	?	?	?	?	?	?	?	?	?	0	-	?
Venenosaurus dicrocei	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Sonorasaurus thompsoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cedarosaurus weiskopfae	?	1	1	1	0	1	1	1	?	?	?	0	-	?
Sauroposeidon proteles	?	?	?	?	?	?	?	?	?	?	?	0	-	1
Tastavinsaurus sanzi	1	1	1	1	0	1	1	1	1	?	0	0	-	1
Huabeisaurus allocotus	?	?	?	?	?	?	?	?	?	?	?	0	-	?
Phuwiangosaurus sirindhornae	?	1	1	?	?	?	?	?	?	?	?	0	-	1
Tangvayosaurus hoffeti	?	1	1	1	0	1	1	1	1	?	?	0	-	1
Yunmenglong ruyangensis	?	?	?	?	?	?	?	?	?	?	?	0	-	?
Qiaowanlong kangxii	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euhelopus zdanskyi	?	1	1	?	?	1	1	?	?	0	?	0	-	1
Erketu ellisoni	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Daxiatitan binglingi	?	?	?	?	?	?	?	?	?	?	?	0	-	?
Chubutisaurus insignis	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Ligabuesaurus leanzai	?	?	?	?	?	?	?	?	?	?	?	0	-	1
Wintonotitan wattsi	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Andesaurus delgadoi	?	?	?	?	?	?	?	?	?	?	?	0	-	?
Rukwatitan bisepultus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mendozasaurus neguyelap	?	?	?	?	?	?	?	?	?	?	?	1	0	1
Malawisaurus dixeyi	?	?	?	?	?	?	1	?	?	?	?	1	0	1
Argentinosaurus huncul**ensis**	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dreadnoughtus schrani	?	?	?	1	?	1	1	?	?	?	?	0	-	1
Epachthosaurus sciuttoi	1	1	1	?	0	1	1	1	1	?	?	0	-	?
Rapetosaurus krausei	?	1	?	?	?	?	?	?	?	?	?	1	0	1
Muyelensaurus pecheni	?	?	?	?	?	?	?	?	?	?	?	?	?	1

Table S.51. Data matrix

Taxa	451	452	453	454	455	456	457	458	459	460	461	462	463	464
Rinconsaurus caudamirus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Overosaurus paradasorum	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Aelosaurus rionegrinus	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Aelosaurus maximus	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Aelosaurus colhuehuapensis	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Tapuiasaurus macedoi	?	1	1	1	0	?	1	1	1	?	?	?	?	?
Gondwanatitan faustoi	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Ampelosaurus atacis	?	?	?	?	?	?	?	?	?	?	?	1	0	?
EC1	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Lirainosaurus astibiae	?	?	?	?	?	?	?	?	?	?	?	1	?	1
Diamantinasaurus matildae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Isisaurus colberti	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Opisthocoelicaudia skarzynskii	1	1	1	1	0	1	1	1	1	0	0	0	-	1
Alamosaurus sanjuanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Saltasaurus loricatus	?	?	?	?	?	?	?	?	?	?	?	1	1	1
Neuquensaurus australis	?	1	?	?	?	?	?	?	?	?	?	1	1	1
Baurutitan britoi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Trigonosaurus pricei	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table S.51. Data matrix

SUPPLEMENTARY MATERIAL 22

Taxa sampling

The following list represent the taxa sampled for the morphological data matrix proposed herein.

Taxon list

Plateosaurus engelhardti Meyer, 1837
Age: Trossingen Formation (Norian).
Material consulted: Carballido and Pol (2010) and Carballido and Sander (2014).

Antetonitrus ingenipes Yates and Kitching, 2003
Age: Lower Elliot Formation (Norian).
Material consulted: Yates and Kitching (2003), Carballido and Pol (2010), Carballido and Sander (2014) and McPhee et al. (2014).

Vulcanodon karibaensis Raath, 1972
Age: Kota Formation (Hettangian).
Material consulted: Raath (1972), Cooper (1984), Wilson (2002), Upchurch et al. (2004a) and Carballido and Sander (2014).

Tazaudosaurus naimi Allain et al, 2004
Age: Azila Formation (Toarcian)
*Material consulted**: Allain and Aquesbi (2008)

Barapasaurus tagorei Jain et al., 1975
Age: Kota Formation (Sinemurian-Aalenian).
Material consulted: Jain et al. (1975, 1979), Wilson (2002), Upchurch et al. (2004a), Bandyopadhyay et al. (2010) and Carballido and Sander (2014).

Shunosaurus lii Dong et al., 1983
Age: Xiashaximiao Formation (Middle Jurassic).
Material consulted: Zhang (1988), Wilson (2002), Upchurch et al. (2004a), Chatterjee and Zheng (2002) and Carballido and Sander (2014).

Cetiosaurus oxoniensis Phillips, 1871
Age: Forest Marble Formation (upper Bajocian-upper Bathonian).
*Material consulted**: OUMNH J13605–13613, J13615–16, J13619–J13688, J13899, J13614, J13617–8, J13780–1, J13596, Upchurch and Martin (2002, 2003), Wilson (2002) and Upchurch et al. (2004a).

Cetiosauriscus stewarti Charig, 1980
Age: Lower Oxfordian Clay (Callovian).
*Material consulted**: NHMUK R3078.

Patagosaurus fariasi Bonaparte, 1979
Age: Cañadón Asfalto Formation (Bajocian-Calovian)
Material consulted: Bonaparte (1986).

Spinophorosaurus nigerensis Remes et al., 2009
Age: Irhazer Group (Bajocian-Bathonian, with doubt).
*Material consulted**: GCP-CV-4229, NMB-1699-R, NMB-1698-R

Omeisaurus spp. Young, 1939
Age: Formation Shangshaximiao (lower Upper Jurassic)
Consulted material: He et al. (1988), Tang et al. (2001), Wilson (2002), Upchurch et al. (2004a), Carballido and Sander, (2014).

Mamenchisaurus spp. Young, 1954
Age: Shangshaximiao and Penglaizhen Formation (lower Upper Jurassic).
Consulted material: Pi et al. (1996), Ouyang and Ye (2002), Wilson (2002), Upchurch et al. (2004a) and Carballido and Sander (2014).

Chuanjiesaurus anaensis Fang et al., 2000
Age: Chuanjie Formation (Middle Jurassic).
Material consulted: Fang et al. (2000) and Sekiya (2011).

Bellusaurus sui Dong, 1990
Age: Formation Wucaiwan (Middle to Late Jurassic).
Consulted material: Dong (1990) and Carballido and Sander (2014).

Lapparentosaurus madagascariensis (Lydekker, 1895)
Age: Isalo III Formation (upper Bathonien).
*Consulted material**: MNHN MAA 91-92, MNHN MAA 1 to MNHN MAA 302.

Jobaria tiguidensis Sereno et al., 1999
Age: Tiourarén Formation (Middle Jurassic to Upper Jurassic; Rauhut and López-Arbarello, 2009; or Aptian-Albian; Sereno et al., 1999)
Consulted material: Sereno et al. (1999), Wilson (2002, 2012), Upchurch et al. (2004a), Whitlock (2011) and Carballido and Sander (2014).

Losillasaurus giganteus Casanovas et al., 2001
Age: Yacimiento de la Cañada (Upper Jurassic-Lower Cretaceous)
*Consulted material**: Lo-1 to Lo-26, Casanovas et al. (2001).

Turiasaurus riodevensis Royo Torres et al., 2006
Age: Villar del Arzobispo Formation (Tithonian-Berriasian)
*Consulted material**: CPT-1195 to CPT-1261, Royo-Torres et al. (2006) and Royo-Torres and Upchurch (2012).

Zby atlanticus Mateus et al., 2014
Age: Praia de Amoreira-Porto Novo (upper Kimmeridgian-basal Tithonian).
*Consulted material**: ML368.

Haplocanthosaurus priscus Hatcher, 1903
Age: Morrison Formation (Kimmeridgian-Tithonian).
Consulted material: Hatcher (1903), Wilson (2002), Upchurch et al., (2004a) and Carballido and Sander (2014).

Amazosaurus maranhensis Carvalho et al., 2003
Age: Itapecuru Formation (Aptian-Albian).
Consulted material: Carvalho et al. (2003), Whitlock (2011) and Carballido et al (2012).

Histriasaurus boscarollii Dalla Vecchia, 1998
Age: Adriatic platform (Hauterivian-Barremian).
Consulted material: Dalla Vecchia (1998), Dalla Vecchia (2005), Apesteguía (2007), Whitlock (2011) and Carballido et al. (2012).

Zapalasaurus bonapartei Salgado et al., 2006
Age: La Amarga Formation (Barremian-Aptian).
Consulted material: Salgado et al. (1996), Whitlock (2011) and Carballido et al. (2012).

Rayososaurus agrioensis Bonaparte, 1996
Age: Candeleros Formation (Cenomanian).
Consulted material: Bonaparte (1996), Whitlock (2011) and Carballido et al. (2012).

Comahuesaurus windhauseni (Carballido et al. 2012.)
Age: Lohan Cura Formation (Aptian-Albian).
Consulted material: Carballido et al. (2012).

Rebbachisaurus garasbae Lavocat, 1954
Age: Formation Tegana (Albian).
*Consulted material**: scapula, and dorsal vertebra of MNHN 1957 and Carballido et al. (2012).

Limaysaurus tessonei (Calvo and Salgado, 1995)
Age: Candeleros Formation and Huincul Formation (Cenomanian).
Consulted material: Calvo and Salgado (1995), Whitlock (2011) and Carballido et al. (2012).

Cathartesaura anaerobica Gallina and Apesteguía, 2005
Age: Huincul Formation (Cenomanian).
Consulted material: Gallina and Apesteguía (2005).

Nigersaurus taqueti Sereno et al., 1999
Age: El Rhaz Formation (Aptian-Albian)
*Consulted material**: MNN GAD512 15-18 and Sereno et al. (1999, 2007) and Carballido et al., 2012.

Demandasaurus darwini Torcida Fernández-Baldor et al., 2011
Age: Castillo de la Reina Formation (Barremian - Aptian)
*Consulted material**: Pereda Suberbiola et al. (2003), Torcida Fernández-Baldor et al., (2011) and Torcida Fernández-Baldor (2012).

Dicraeosaurus spp. Janensch, 1914
Age: Tendaguru Formation (Kimmeridgian)
*Consulted material**: Skeleton M, E, o, Ob and other material referred in Janensch (1929, 1961).

Brachytrachelopan mesai Rauhut et al., 2005
Age: Cañadón Calcáreo Formation (Kimmeridgian - Tithonian).
Consulted material: Rauhut et al. (2005), Whitlock (2011) and Carballido et al. (2012).

Amargasaurus cazaui Salgado and Bonaparte, 1991
Age: La Amarga Formation (Barremian-Aptian)
Consulted material: Salgado and Bonaparte (1991), Wilson (2002), Whitlock (2011), Carballido et al. (2012) and Carabajal et al. (2014).

Suuwassea emilieae Harris and Dodson, 2004
Age: Morrison Formation (Tithonian)
Consulted material: Harris and Dodson (2004), Harris (2006a, b, c), Whitlock and Harris (2010), Whitlock (2011), Carballido and Sander (2014) and Tschopp et al. (2015).

Apatosaurus spp. Marsh, 1877
Age: Morrison Formation (Tithonian)
*Consulted material**: LACM 52844, Gilmore (1936), Wilson (2002), Upchurch et al., (2004a, b), Whitlock (2011), Carballido and Sander (2014) and Tschopp et al. (2015).

Tornieria africana (Fraas, 1908)
Age: Tendaguru Formation (Tithonian)
*Consulted material**: MB.R.2728 (A 4), MB.R.2672 (A 1), MB.R.2713 (A 4), MB.R.2386 (k 1), k3, k ?, MB.R.2730 (k 34), MB.R.2726 (k 35), MB.R.2673 (k 37), MB.R.2586 (k 38), MB.R.2733 (k 44), MB.R.2669 (k 40), and MB.R.2572 (k 41), MB.R.2956.1-24, MB.R.2957, and MB.R.2958, 26 anterior and mid-caudal vertebrae from trench dd, Remes et al., (2006).

Supersaurus vivianae Jensen, 1985
Age: Morrison Formation (Kimmeridgian-Tithonian)
Consulted material: Jensen (1985), Lovelace et al. (2007), Whitlock (2011), Mannion et al. (2012), Tschopp et al. (2015).

Kaatedocus siberi Tschopp and Mateus, 2013
Age: Morrison Formation (Kimmeridgian-Tithonian)
Consulted material: Tschopp and Mateus, 2013

Barosaurus spp. Marsh, 1890
Age: Morrison Formation (Kimmeridgian)
Consulted material: Lull (1919), McIntosh (2005), Whitlock (2011) and Tschopp et al. (2015).

Diplodocus spp. Marsh, 1878
Age: Morrison Formation (Kimmeridgian-Tithonian)
*Consulted material**: MNCN 63731 ("Dippy" cast), Osborn (1899), Hatcher (1901), Wilson (2002), Whitlock (2011), Carballido and Sander (2014) and Tschopp et al. (2015).

Dinheirosaurus lourinhanensis Bonaparte and Mateus, 1999
Age: Praia de Amoreira-Porto Novo (upper Kimmeridgian-basal Tithonian), very close to the overlying Sobral Formation (upper Kimmeridgian-lower Tithonian).
*Consulted material**: ML 414 (including unpublished and undescribed bones) and field information, Bonaparte and Mateus (1999) and Mannion et al., (2012).

SHN (JJS) 177 (this work)
Age: Praia de Amoreira-Porto Novo (upper Kimmeridgian-basal Tithonian).
*Consulted material**: SHN (JJS) 177.

Camarasaurus spp. Cope, 1877
Age: Morrison Formation (Kimmeridgian-Tithonian)
Consulted material: Osborn and Mook (1921), Ostrom and McIntosh (1966), McIntosh et al. (1996a, b), Wilson (2002), Ikejiri (2004), Ikejiri et al. (2005) and Carballido and Sander (2014).

Lourinhasaurus alenquerensis (Lapparent and Zbyszewski, 1957)
Age: Sobral Formation (lower Tithonian)
*Consulted material**: MG 4956, MG 30373, MG 30377, MG 30379, MG 4956, MG 30378, MG 30384, MG 30370, MG 4956, MG 30380, MG 30376, MG 4956, MG 30374, MG 30388, MG 30387, MG 5780, MG 30371, MG 5780, MG 30372, MG 30383, MG 30382, MG 2, MG 30381, MG 4979, MG 4979, MG 30385, MG 5781, MG 4975, MG 4970, MG 4957, MG 4931, MG 4983, MG 4984, MG 30375, MG 30386 and unlabelled fragmentary elements.

SHN 181 (this work)
Age: Praia de Amoreira-Porto Novo Formation (upper Kimmeridgian-basal Tithonian).
Consulted material: SHN 181.

Tehuelchesaurus benitezi Rich et al. (1999)

Age: Cañadón Calcáreo Formation (Kimmeridgian-Tithonian).

*Consulted material**: Rich et al. (1999), Carballido et al. (2011).

Aragosaurus ischiaticus Sanz et al. (1987)

Age: Villar del Arzobispo Formation (Tithonian-Berriasian)

*Consulted material**: I.G. 468 (V40), I.G. 481 (Cos), I.G. 487 (Phs1), I.G. 492 (Uls), V20, I.G. 453 (V8), I.G. 473 (V1), I.G. 474 (V2s), I.G. 450 bis (V5), I.G. 475 (V3), I.G. 476 (V4), I.G. (477 (V5), I.G. 479 (V7), I.G. 480 (V8), ZH-18, ZH-17, ZH-12, ZH-15, ZH-16, I.G. 468 (V55 and X3), I.G. 493 (V9s), ZH-4, ZH-5, ZH-7, ZH-8, ZH-9, ZH-11, ZH-13, ZH-14, ZH-1, I.G. 482 (Oms), I.G. 482 (Oms), I.G. 490 (Fes), I.G. 483 (Cu), I.G. 484 (Ra), I.G.485 (Cars), I.G. 486 (rmc1), I.G. 486 (rmc2), I.G. 486 (rmc3), I.G. 486 (rmc4), I.G. 489 (Pus), Zh-3, I.G. 492 (Uls), I.G. 488 (Is), Zh-2, Zh-6, Zh-10 and Zh-19.

Europasaurus holgeri Sander et al., 2006

Age: Saxony Basin (middle Kimmeridgian)

*Consulted material**: DFMMh/FV 291.18, DFMMh/FV 291.17, DFMMh/FV 291.25, DFMMh/FV 291.15, DFMMh/FV 291.16, DFMMh/FV 291.10, DFMMh/FV 291.24, DFMMh/FV 291.11, DFMMh/FV 291, DFMMh/FV 291, DFMMh/FV 291.34, DFMMh/FV 1029, DFMMh/FV288, 1034.2, 187, DFMMh/FV 1077, 581.1, DFMMh/FV 33, 92, 93, 290, 654, 1058.14, DFMMh/FV 34, 59, 94, 501, 653, 834.7, DFMMh/FV 965.4, 748, 966, DFMMh/FV 162, 389, 907, DFMMh/FV 552, DFMMh/FV 1083, 789, DFMMh/FV 100.4, 292, DFMMh/FV 521, 994, 858.2, DFMMh/FV 77, 911, 218, DFMMh/FV 831, 1037.13, 867.4, DFMMh/FV 785.4, 897, DFMMh/FV 169, 1078, 581.2, DFMMh/FV 883, 581.3, DFMMh/FV 95. 380, 97, 98, 555.1, DFMMh/FV 96, DFMMh/FV 520, 837.4, DFMMh/FV 703.5, 32, 831, 890.8, 982, DFMMh/FV 61, 652.2, DFMMh/FV 100.2, 244, 554.6, 965.4, 748, DFMMh/FV 196, 966, DFMMh/FV 62, 785.2, DFMMh/FV 58, 57, 972.2, 1032.2, DFMMh/FV 734, DFMMh/FV 100.1, DFMMh/FV 704, 657, 712.2, 993, 1004, DFMMh/FV 41, 867.3, 724, 723, DFMMh/FV 713, 785.3, 838.3, DFMMh/FV 100.5, 100.6, 100.7, 278, 280, 291.33, 422-430, 431-462, 472, 478, 479, 486-489, 492.8, 495.6, 496, 504, 516, 537, 559, 578.6, 580.1, 602, 606, 607, 636, 660, 662, 663, 707.3.1, 707.3.2, 709.2, 726, 727, 730, 731, 771, 788, 790.6, 790.7, 844.7, 848, 851, 860, 865.1, 865.1, 867 ,6, 868.2, 869, 876, 882, 889, 896.7.1, 896.7.2, 896.7.3, 900, 948.), DFMMh/FV 910, 204, 362, 775, 791, DFMMh/FV 563.2, 706.1, DFMMh/FV 857.3, 785.1, 46, 119, 126, 127, 652.1, 701.1, 857.1, 896.8, 554.8, DFMMh/FV 710, DFMMh/FV 873.1, 867.8, 573.6, DFMMh/FV 894, 1048, 833.4, 550.1, DFMMh/FV 835, 1049, 787, DFMMh/FV 712.1, 652.4, 890.1, 007, 580.2, 012, 019, 723, DFMMh/FV 857.3, 119, 1031, 833.1, DFMMh/FV 51, DFMMh/FV 51, 126, 783, 836.2, 857.1, 785.1, 554.8, DFMMh/FV 857.2, 243, [1032, 1072], DFMMh/FV 120, 128, 18, 129, 130, 246, 243, DFMMh/FV 100, 082, 890.3-5, 569, 563.3, 890.7, 834.4, 553.2, 862, 20, 875.2, 182, 206, 285, 862, 866, DFMMh/FV 132, 716, 717, 240, 782, 133, 134, 495.3, 884, 743, 775, DFMMh/FV 286, 716, 718, 837.2, 546, 553.1, 700.2, 558.3, 781, 719, 180, DFMMh/FV 784, 844.4, 745, 744, 549.2, 548, 882, 549.1, 47, 565.2, DFMMh/FV 544, 836.1, 163, 896.1, 890.6, 857.5, 652.10, 652.11, 834.3-6, 469, 179, 739, 732, DFMMh/FV 555.4, 542, 652.3, 652.12, 873.3, 862.1, 708, 774, 512, 652.9, 652.13, 428, 834.2, 701.2, 702.2, 85, 412, 38, 143, 91 and Sander et al. (2006), Carballido and Sander (2014) and Marpmann et al. (2015).

Galveosaurus herreroi Sánchez-Hernández (2005)

Age: Villar del Arzobispo Formation (Tithonian).

*Consulted material**: GAL00/CL/48, 181, 86, 62, 90, 102, 35 and from Barco (2009).

Lusotitan atalaiensis (Lapparent and Zbyszewski, 1957)
Age: Sobral Formation (lower Tithonian)
*Consulted material**: MG 3794, MG 4798, MG 4801, MG 4805-10, MG 4838, MG 4944, MG 4950, MG 4952, MG 4958, MG 4964, MG 4965, MG 4966, MG 4981, MG 4982, MG 4803, MG 4985-1, MG 4985 2-20, MG 5795, MG 8793, MG 8794, MG 8807 and unlabeled sacral neural spine and chevron

Brachiosaurus altithorax Riggs, 1903
Age: Morrison Formation (Kimmeridgian-Tithonian)
Consulted material: Riggs (1903), Taylor (2009), Mannion et al. (2013) and Carballido and Sander (2014) and photos of FMNH P 25107.

Giraffatitan brancai (Janensch, 1914)
Age: Tendaguru Formation (Kimmeridgian-Tithonian)
*Consulted material**: HMN SII and HMN SI and referred material (see Janensch, 1961).

Abydosaurus mcintoshi Chure et al., 2010
Age: Cedar Mountain Formation (Albian).
*Consulted material**: Chure et al. (2010) and Mannion et al. (2013).

Venenosaurus dicrocei Tidwell et al., 2001
Age: Cedar Mountain Formation (Barremian).
Consulted material: Tidwell et al. (2001), Tidwell and Wilhite (2005) and D'Emic (2012).

Cedarosaurus weiskopfae Tidwell et al., 1999
Age: Cedar Mountain Formation (Barremian)
Consulted material: Tidwell et al. (1999), D'Emic (2012, 2013) and Carballido and Sander (2014).

Sonorasaurus thompsoni Ratkevich, 1998
Age: Turney Ranch Formation (Late Albian–early Cenomanian)
Consulted material: Ratkevich (1998), D'Emic (2012) and Mannion et al. (2013).

Sauroposeidon proteles Wedel et al. (2000a)
Age: Twin Mountains Formation (Aptian-Albian)
Consulted material: Wedel et al. (2000a, b), Rose (2007), D'Emic (2012), D'Emic and Foreman (2012), Carballido and Sander (2014).

Tastavinsaurus sanzi Canudo et al., 2008
Age: Xert Formation (Aptian)
*Consulted material**: Arsis1-134, Ars1-77-79, Ars1-53, Ars1-57, Ars69, Ars74, Ars85, Ars86, Ars88-91, Ars1-19, Ars1-7, Ars1-80, Ars1-83, Ars1-10, Ars1-26, Ars1-27, Ars1-30, Ars1-31, Ars1-33, Ars1-35, Ars1-36, Ars1-39, Ars1-40-42, Ars1-45, Ars1-47-49, Ars1-51, Ars1-62-65, Ars1-70-73), Ars1-15, Ars1-22, Ars1-28, Ars1-32, Ars1-34, Ars1-37, Ars1-38, Ars1-43, Ars1-44, Ars1-46, Ars1-55, Ars1-56, Ars1-59, Ars1-60, Ars1-61, Ars1-66-68, Ars1-75, Ars1-81, Ars1-82, Ars1-9, Ars1-58, Ars1-16, Ars1-84, Ars1-23, Ars1-24, Ars1-6, Ars1-76, Ars1-50, Ars1-54, Ars1-134, Ars1-4, Ars1-5, Ars1-8, Ars1-11, Ars1-52, Ars1-21, Ars1-2, Ars1-29, Ars1-110, Ars1-133, Ars1-12, Ars1-13, Ars1-87, Ars1-3, CPT-839e847, CPT-850e852, CPT-856, CPT-861, CPT-862, CPT-870, CPT-884, CPT-3213, CPT-3214, CPT-885, CPT-883, CPT-837, CPT-88, CPT-886, CPT-848, CPT-849, 882, CPT-838, CPT-859, CPT-874, CPT-3374, CPT-880, CPT-863, CPT-866, CPT-3373, CPT-867, CPT-868, CPT-864, CPT-865, CPT-871, CPT-876e879, CPT-881, CPT-3370, CPT-3371.

Huabeisaurus allocotus Pang and Cheng, 2000
Age: Huiquanpu Formation (?Cenomanian-?Campanian).
Consulted material: D'Emic et al. (2013).

Phuwiangosaurus sirindhornae Martin et al., 1994
Age: Sao Khua Formation (Barremian-Aptian)
Consulted material: Martin (1994), Martin et al. (1999), Suteethorn et al. (2009), Suteethorn et al. (2010), Mannion et al. (2013) and Carballido and Sander (2014).

Tangvayosaurus hoffeti Allain et al., 1999
Age: Grès supérieurs Formation (Aptian-Albian).
Consulted material: Allain et al. (1999), Suteethorn et al. (2009), Suteethorn et al. (2010), D'Emic (2012) and Mannion et al. (2013).

Yunmenglong ruyangensis Lü et al. (2013)
Age: "Mangchuan Formation" (upper Lower Cretaceous-lower Upper Cretaceous).
Consulted material: Lü et al. (2013).

Qiaowanlong kangxii You and Li, 2009
Age: Xinminpu Group (Aptian-Albian).
Consulted material: You and Li (2009), D'Emic (2012) and Mannion et al. (2013).

Euhelopus zdanskyi (Wiman, 1929)
Age: Mengyin Formation (Barremian-Aptian).
Consulted material: Wiman (1929), Wilson (2002), Wilson and Upchurch (2009), Carballido et al. (2012) and Poropat and Kear (2013)

Erketu ellisoni Ksepka y Norell, 2006
Age: Baynshiree Formation (early Upper Cretaceous).
Consulted material: Ksepka and Norell (2006, 2010), Carballido et al. (2012), Wilson et al. (2011) and Mannion et al. (2013).

Daxiatitan binglingi You et al., 2008
Age: Hekou Group (Lower Cretaceous).
Consulted material: You et al. (2008), D'Emic (2012) and Mannion et al. (2013).

Chubutisaurus insignis del Corro, 1975
Age: Cerro Barcino Formation (Cenomanian).
Consulted material: del Corro (1975), Carballido et al. (2011b, 2012).

Ligabuesurus lenzai Bonaparte et al., 2006
Age: Lohan Cura Formation (Aptian-Albian).
Consulted material: Bonaparte et al. (2006), Carballido et al. (2012) and Mannion et al. (2013).

Wintanotitan wattsi Hocknull et al. 2009
Age: Winton Formation (Cenomanian-?Turonian).
Consulted material: Hocknull et al. (2009) and Poropat et al. (2014).

Andesaurus delgadoi Calvo and Bonaparte, 1991
Age: Candeleros Formation (Cenomanian).
Consulted material: Calvo and Bonaparte (1991), Mannion and Calvo (2011) and Carballido and Sander (2014)

Rukwatitan bisepultus Gorscak et al. 2014
Age: Galula Formation (Aptian-Cenomanian).
Consulted material: Gorscak et al. 2014.

Mendozasaurus neguyelap Gonzáles Riga, 2003
Age: Formation Río Neuquén (Turonian-Coniacian).
Consulted material: González Riga (2003) and Carballido et al. (2012).

Malawisaurus dixeyi (Haughton, 1928)
Age: "Dinosaur Beds" (Aptian).
Consulted material: Jacobs et al. (1993), Gomani (1999, 2005) and Carballido and Sander (2014).

Argentinosaurus huinculensis Bonaparte and Coria, 1993
Age: Huincul Formation (Albian-Cenomanian).
Consulted material: Bonaparte and Coria (1993) and Carballido and Sander (2014).

Dreadnoughtus schrani Lacovara et al., 2014
Age: Cerro Fortaleza Formation (Campanian–Maastrichtian).
Consulted material: Lacovara et al. (2014).

Epachthosaurus sciuttoi Powell, 1990
Age: Bajo Barreal Formation (Cenomanian-Turonian)
Consulted material: Martínez et al. (2004), Giménez (2008) and Carballido et al. (2012).

Rapetosaurus krausei Curry Rogers and Foster, 2001
Age: Maevarano Formation (Maastrichtian)
Consulted material: Curry Rogers and Foster (2001, 2004), Curry Rogers (2005, 2009) and Carballido et al. (2012).

Muyelensaurus pecheni Calvo et al., 2007
Age: Portezuelo Formation (upper Turonian-lower Coniacian).
Consulted material: Calvo et al. (2007) and Santucci and Arruda-Campos (2011).

Rinconsaurus caudamirus Calvo and González Riga, 2003
Age: Río Neuquén Formation (upper Turonian-lower Coniacian).
Consulted material: Calvo and González Riga (2003) and Santucci and Arruda-Campos (2011).

Overosaurus paradasorum Coria et al., 2013
Age: Anacleto Formation (Campanian).
Consulted material: Coria et al. (2013).

Aelosaurus rionegrinus Powell, 1987
Age: Angostura Colorada Formation (upper Campanian-lower Maastrichtian).
Consulted material: Powell (1987) and Santucci and Arruda-Campos (2011).

Aelosaurus maximus Santucci and Arruda-Campos, 2011
Age: Adamantina Formation (Campanian–Maastrichtian).
Consulted material: Santucci and Arruda-Campos (2011).

Aelosaurus colhuehuapensis Casal et al., 2007
Age: Formación Bajo Barreal (Senonian).
Consulted material: Casal et al. (2007) and Santucci and Arruda-Campos (2011).

Gondwanatitan faustoi Kellner and Azevedo, 1999
Age: Adamantina Formation (Campanian–Maastrichtian).
Consulted material: Kellner and Azevedo (1999) and Santucci and Arruda-Campos (2011).

Ampelosaurus atacis Le Loeuff, 1995
Age: Marnes Rouges Inférieures Formation (upper Campanian-lower Maastrichtian).
*Consulted material**: Le Loeuff (1995, 2005).

EC1 skeleton from "Lo Hueco" quarry (Spain).
Age: "Margas, Arcillas y Yesos de Villalba de la Sierra" Formation (upper Campanian-lower Maastrichtian).
*Consulted material**: EC1.

Isisaurus colberti (Jain and Bandyopadhyay, 1997)
Age: Lameta Formation (Maastrichtian)
Consulted material: Jain and Bandyopadhyay (1997), Wilson and Upchurch (2003) and Carballido and Sander (2014).

Lirainosaurus astibiae Sanz et al., 1999
Age: Sedano Formation (upper Campanian-lower Maastrichtian).
*Consulted material**: Sanz et al. (1999), Díez-Díaz et al. (2011, 2012, 2013a, b).

Diamantinasaurus matildae Hocknull et al., 2009
Age: Winton Formation (Cenomanian-?Turonian).
Consulted material: Hocknull et al. (2009) and Poropat et al. (2014).

Opisthocoelicaudia skarzynskii Borsuk-Bialynicka, 1977
Age: Nemegt Formation (Campanian-Maastrichtian)
Consulted material: Borsuk-Bialynicka (1997), Wilson (2002), Carballido et al. (2012) and Mannion et al. (2013).

Alamosaurus sanjuanensis Gilmore, 1922
Age: North Horn Formation (Campanian-Maastrichtian)
Consulted material: Lehman and Coulson (2000), Wilson (2002), Carballido et al. (2012), Poropat et al. (2015) and Mannion et al. (2013).

Neuquensaurus australis (Lydekker, 1893)
Age: Anacleto Formation (Campanian).
Consulted material: Powell (2003), Otero (2010) and Carballido et al. (2012).

Saltasaurus loricatus Bonaparte and Powell, 1980
Age: Lecho Formation (Campanian-Maastrichtian)
*Consulted material**: Powell (1992, 2003) and Zurriaguz and Powell (2015).

Baurutitan britoi Kellner et al., 2005
Age: Marília Formation (Maastrichtian).
Consulted material: Kellner et al. (2005) and Santucci and Arruda-Campos (2011).

Trigonosaurus pricei Campos et al., 2005
Age: Marília Formation (Maastrichtian).
Consulted material: Powell (2003), Campos et al. (2005) and Carballido et al. (2012).

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SUPPLEMENTARY MATERIAL 23

Map of synapomorphies of Chapter 13 phylogenetic approach

Synapomorphies for the nodes of Chapter 13 phylogenetic approach

Node 1, Sauropoda. No synapomorphies.

Node 2. 323 (0→1), 324 (0→1), 328 (0→1), (345 (0→), 398 (0→), 451 (0→1).

Node 3. 421 (0→1), 434 (0→1), 455 (0→1).

Node 4. 168 (0→1), 193 (0→1), 381 (0→1), 406 (0→1), 409 (0→1), 412 (0→1), 420 (0→1), 441 (0→1), 454 (0→1).

Node 5. Eusauropoda. 168 (0→1), 196 (0→1), 305 (0→1).

Node 6. 1 (0→1), 68 (0→1), 144 (0→1), 165 (0→1), 187 (0→1), 224 (1→2), 229 (0→1).

Node 7. 193 (1→0), 197 (1→0), 402 (0→1).

Node 8. 263 (0→1).

Node 9. 160 (0→1), 268 (1→0), 309 (0→1).

Node 10, Mamenchisauridae. 119 (0→1), 171 (0→2), 231 (1→0), 294 (1→0), 306 (0→1), 400 (1→0), 403 (0→1).

Node 11. 111 (0→1), 115 (1→4), 124 (0→2), 141 (0→1), 142 (1→0), 143 (0→1), 168 (1→0), 209 (0→2), 263 (1→0), 430 (1→0).

Node 12. 183 (0→1), 234 (0→1), 240 (0→3).

Node 13. 31 (0→1), 121 (0→1), 125 (0→1), 179 (0→1), 278 (2→1), 350 (0→1), 351 (0→1), 387 (0→1), 433 (0→1).

Node 14. Turiasauria. 77 (0→1), 207 (0→1), 209 (0→1), 326 (0→1), 329 (0→1), 333 (0→1), 337 (0→1).

Node 15. 347 (0→1).

Node 16. 180 (0→1), 415 (0→1), 417 (0→1).

Node 17. 165 (1→0), 210 (1→0), 216 (0→1).

Node 18. 124 (0→1), 132 (1→0), 162 (0→1), 292 (0→1).

Node 19, Neosauropoda. 119 (0→1), 167 (0→1), 171 (0→1), 253 (0→1).

Node 20, Diplodocoidea. 1 (1→0), 2(1→0), 7 (0→1), 9 (0→1), 19 (0→1), 20 (0→1), 22 (0→1), 57 (0→1), 62 (1→2), 82 (0→1), 99 (1→2), 100 (1→3), 102 (0→1), 105 (1→0), 108 (1→2), 113 (0→3), 145 (1→0), 174 (1→0), 177 (1→2), 196 (1→0), 206 (0→2), 216 (0→1), 227 (0→1), 254 (0→1), 261 (0→1), 264 (0→1), 268 (0→1), 277 (0→1), 281 (0→1), 282 (0→1), 284 (0→1).

Node 21, Rebbachisauridae. 259 (1→0), 271 (0→1).

Node 22. 133 (0→2), 199 8(0→1), 214 (0→1), 236 (0→1), 240 (0→4).

Node 23, Limaysaurinae. 183 (0→2), 208 (0→1), 306 (0→1).

Node 24. 307 (0→1).

Node 25, Nigersaurinae. 183 (0→1), 190 (0→1), 249 (0→1), 265 (0→1), 389 (0→1), 413 (0→1).

Node. 26, Flagellicaudata. 8 (0→1), 12 (1→2), 55 (1→0), 60 (0→1), 86 (0→1), 104 (0→1), 141 (0→1), 190 (0→1), 215 (0→1), 240 (0→2), 278 (1→2), 292 (1→0), 387 (1→0), 388 (0→1), 396 (1→0); 444 (0→1).

Node 27, Dicraeosauridae. 4 (0→1), 26 (0→1), 34 (1→0), 45 (0→1), 52 (0→1), 88 (0→1), 89 (0→1), 157 (0→1), 160 (1→0).

Node 28. 35 (0→1), 49 (0→1), 125 (1→0), 150 (0→1), 165 (1→0), 171 (1→0), 217 (1→2).

Node 29. 204 (0→1).

Node 30, Diplodocidae. 25 (0→1), 28 (0→1), 46 (0→1), 106 (1→0), 115 (1→3), 124 (1→2), 155 (0→1), 164 (2→4), 168 (1→0), 184 (0→1), 185 (0→1), 251 (0→1), 257 (0→1), 258 (0→1), 262 (0→1).

Node 31, Diplodocinae. 134 (0→1), 143 (0→1), 146 (0→1), 151 (0→1), 154 (0→1), 161 (0→1), 243 (0→1), 245 (0→1), 246 (0→1), 247 (0→1), 266 (0→1), 271 (0→2), 274 (2→3), 305 (1→0), 306 (0→1), 403 (0→1), 411 (0→1).

Node 32. 126 (0→1), 153 (0→1), 156 (0→1), 267 (0→1), 269 (0→1).

Node 33. 155 (1→0), 194 (0→1).

Node 34. 248 (0→1).

Node 35, Macronaria. 121 (1→2), 168 (1→0), 195 (0→1), 209 (0→2), 306 (0→1), 382 (0→1), 386 (0→1).

Node 36, Camarasauromorpha. 162 (1→0).

Node 37, Camarasauridae. 174 (1→0), 177 (1→0).

Node 38. 215 (0→1), 302 (0→1), 397 (0→1).

Node 39. 259 (1→0), 296 (0→1), 355 (0→1).

Node 40. 379 (0→1), 390 (0→1).

Node 41. 253 (1→0), 293 (0→1).

Node 42, Titanosauriformes. 105 (1→0), 124 (1→2), 143 (0→1), 211 (0→1), 252 (0→1), 287 (0→1), 335 (1→0), 408 (1→2).

Node 43, Brachiosauridae. 2 (1→2), 141 (0→1), 175 (1→0), 180 (1→0), 220 (0→1), 237 (0→1), 239 (0→1), 244 (0→1), 259 (0→1), 288 (0→1), 323 (1→2), 364 (0→1), 367 (0→1), 417 (0→1), 418 (0→1), 450 (0→1).

Node 44. 234 (0→2), 274 (2→0), 449 (0→1).

Node 45. 259 (1→0), 279 (0→1).

Node 46. 171 (1→2), 272 (0→1).

Node 47. 160 (0→1), 171 (1→2), 308 (0→1), 331 (0→1), 338 (0→1), 402 (0→1), 423 (0→1).

Node 48. 121 (2→3), 125 (1→0), 144 (1→0), 167 (1→0), 189 (0→1).

Node 49. 332 (0→1), 449 (0→1).

Node 50. 218 (0→1), 309 (1→0), 384 (0→1).

Node 51, Somphospondyli. 287 (1→0), 376 (0→1).

Node 52, Euhelopodidae. 134 (0→1), 219 (1→0).

Node 53. 271 (0→1).

Node 54. 158 (0→1), 382 (1→0), 384 (1→0).

Node 55. 121 (3→1), 128 (0→1).

Node 56. 123 (1→0), 166 (0→1), 168 (0→1), 306 (0→1), 312 (1→0), 402 (1→0), 403 (0→1), 404 (1→0).

Node 57, Titanosauria. 166 (0→1), 176 (0→1), 337 (0→1).

Node 58, Lithostrotia. 179 (1→2), 180 (1→2), 182 (0→1), 183 (0→2), 241 (0→1), 462 (0→1).

Node 59. 122 (0→1), 327 (0→1).

Node 60. 238 (0→1), 239 (0→1), 272 (0→2).

Node 61. 160 (1→0), 172 (1→0), 173 (1→0), 198 (0→1), 272 (0→3), 279 (0→1), 416 (0→1).

Node 62, Aelosaurini. 34 (1→0), 170 (1→0), 193 (1→0), 196 (1→0).

Node 63, Rinconsauria. 108 (2→0), 169 (0→1), 202 (1→0), 241 (1→0), 289 (0→1).

Node 64. 208 (0→1), 247 (0→1), 275 (0→1).

Node 65. 276 (1→2).

Node 66. 241 (1→0), 255 (0→1), 274 (2→0).

Node 67. 244 (0→1), 270 (0→1).

Node 68. 187 (1→0), 233 (1→2), 315 (0→1), 344 (1→0), 369 (0→1), 370 (0→1).

Node 69. 195 (1→0), 202 (1→0), 205 (0→1), 206 (1→2), 270 (0→1), 288 (0→1), 338 (1→0), 423 (1→0).

Node 70. 182 (1→0).

Node 71. 286 (0→1), 313 (0→1), 327 (0→1), 334 (0→1), 347 (0→1), 418 (0→1).

Node 72. 173 (0→1), 180 (2→1), 274 (2→1).

Node 73. 182 (1→0), 183 (2→0), 416 (1→0).

Node 74. 241 (1→0), 245 (0→1), 253 (0→1).

Node 75, Saltasauridae. 246 (0→1), 247 (0→1), 276 (1→0).

Node 76, Saltasaurinae. 178 (0→1), 179 (0→1), 202 (1→0), 250 (0→1), 280 (0→1), 288 (0→1), 411 (0→1).

Node 77, Ophistocoelicaudinae. 181 (1→2), 211 (1→0), 309 (0→1), 310 (1→0), 378 (0→1), 402 (1→0), 417 (0→1).

Node 78. 179 (2→1), 218 (1→0), 313 (1→0), 334 (1→0), 365 (1→0).

Node 79. 189 (2→0), 195 (2→0), 202 (1→0), 327 (1→0), 330 (0→1).

Note: This map of synapomorphies was obtained from the topology of consensus strictus.

Figure S.9. Phylogenetic hypothesis obtained in the chapter 13 up to Macronaria clade (the cladogram continues on Figure S.10)

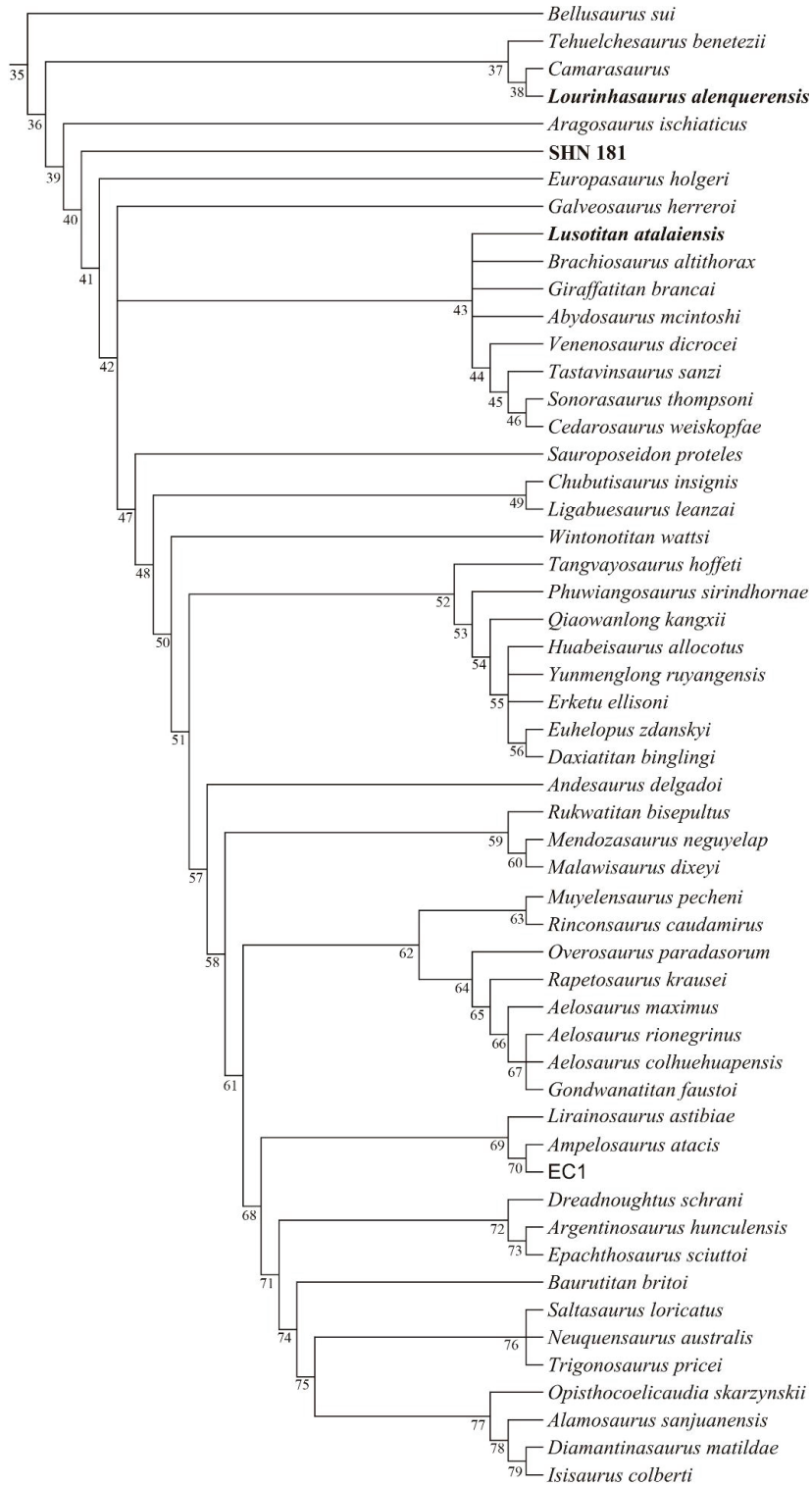

Figure S.10. Phylogenetic hypothesis obtained in the chapter 13 for macronarians